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CONTENTS

Lichens—Their Biological and Economic Significance.
GEORGE ALBERT PEREZ-LLANO 1

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THE BOTANICAL REVIEW

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LICHENS
THEIR BIOLOGICAL AND ECONOMIC SIGNIFICANCE[1]

GEORGE ALBERT PEREZ-LLANO
Harvard University

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PREFACE

The principal purpose of this paper is to consider the economic uses of lichens. Because the general student may have had little association with lichenology, it is felt, however, that a preliminary discussion of the more important biological aspects might be helpful.

Lichenology is a large and specialized field which this paper cannot hope to encompass. Therefore, the material presented in the first part is, necessarily, of a very limited nature. It consists of a compilation of papers dealing with the morphology, symbiosis, reproduction, growth, physiology, taxonomy, distribution, ecology and origin of lichens, with special emphasis on publications since 1921. Because it has been possible to examine only part of the most recent literature, the data of A. L. Smith's book "Lichens" have been chosen as the most convenient, for it reviews all previous work in great detail and includes a full bibliography, notably on the older works. Nevertheless, in some cases it has been found essential to refer to publications prior to 1921. This is true, chiefly, of the latter part of the paper, for the endeavor here is to bring together all information available pertaining to economic and industrial uses of these plants.

I am indebted to many, particularly Dr. P. F. Scholander, for valued suggestions and criticisms. To Dr. K. V. Thimann, Dr. D.

H. Linder, Dr. W. H. Weston, Dr. P. C. Mangelsdorf, Dr. A. H. Hill, who have been kind enough to read part or all of this manuscript, I express my very deep appreciation, but at the same time absolve them all from responsibility for errors that may appear.

BIOLOGY

Lichens are plants consisting of light-colored hyphal filaments and cells or groups of cells of a green, blue-green, or more rarely brownish or reddish color. The green bodies and hyphal filaments are in close relationship with each other and contribute to the formation of a quite constant structure, the thallus, which in form varies according to habitat. Lichens are found on a wide variety of substrata, from the High Arctic to the Tropics and from mountain top to seashore, contributing richly, in some cases, to the flora of a region. The total number of known species is over 15,500, comprising 60 families and over 400 genera (232).

Morphology

Macroscopic Structure. Though the thallus may range in shape from leaf-like to filamentous or even to a powder-like entity, it is generally classified into one of three types—foliose, fruticose or crustose. The fruticose type may be somewhat specialized, so that the erect thallus is referred to as the podetia[2], with superficial outgrowths known as squamules[3]. In size, the lichen thallus varies from the obvious to the microscopic. The dorsal surface may be smooth to pustulate and may bear outgrowths such as cilia, isidia[4], branchlets, or cephalodia[5]; the last occasionally occurring below the thallus surface.

The spermagonia[6] or male reproductive bodies which bring about fertilization resulting in formation of the fruit or apothecia, and the soredia[7] are also usually to be seen on the upper surface, while the lower surface may have cyphellae or breathing pores

[2] Podetia: alga-bearing branched or unbranched stalks, rising from the primary or horizontal thallus in certain lichens and bearing the ascocarp.
[3] Squamule: a small scale.
[4] Isidia: coral-like outgrowths on thalli in foliose and fruticose forms.
[5] Cephalodia: small regular or irregular outgrowths appearing on the surface of a few lichen thalli, containing algal cells and hyphae, usually enclosed finally in plectenchymatous cortex (63).
[6] Spermagonia: it appears to the writer that this customary spelling is incorrect and should be spermatogonia.
[7] Soredia: the accepted spelling of this word is incorrect; should be soridia.

as well as cilia and the coarser rhizinae. The hypothallus is the first growth of the thallus before differentiation; it persists as a dark, ring-like, marginal outgrowth common to some crustaceous forms; its function is not very clear.

Microscopic Structure.

a. Foliose Lichens. The green bodies and the colorless hyphal filaments may be interspersed through the entire thallus ("homoeomerous") or they may be arranged in distinct layers ("heteromerous") so as to present a false parenchyma-like appearance. In the heteromerous type of thallus there is an upper cortex consisting of more or less vertical hyphae without intercellular spaces; its surface may or may not be externally limited by an epidermis-like layer of hyphae (dermis). Beneath this there is an area of interwoven hyphae in which the intermingled green cells are enclosed. These cells were once thought to be the reproductive parts of the plants and were described as "gonidia" if green, or "gonimia" if blue-green. Because of this the green zone is often referred to as the "gonidial layer" or, more recently, as the "algal layer". The third layer is the medulla composed of loosely interwoven hyphae beneath which there is a compacted layer of hyphae, the lower cortex, and from this the rhizinae grow out. This is, in general, the microscopic structure of the foliose lichen thallus; to a certain extent, this is the structure in crustose and fruticose lichen thalli also, though, owing to their habit of growth, variation and intergradation occur.

b. Crustose Lichens. Crustose lichens growing over rock surfaces are referred to as "epilithic" or, if penetrating their substratum, as "endolithic" forms; both together come under the grouping of "saxicolous" lichens. If the substratum is wood or bark, the thallus may be immersed ("hypophloeodal") or growing only on the surface ("epiphloeodal"), and in either case it is known as a "corticolous" lichen. Because of their peculiar type of habitat, the thallus is considerably modified and may range from the homoeomerous to the heteromerous type of structure.

c. Fruticose Lichens. The fruticose lichen thallus, because of its more or less cylindrical form, appears somewhat more specialized. It consists of an outer pseudocortex of densely interwoven hyphae extending either in the direction of the axis or at right

angles to it. Within this is the algal layer which may be evenly disposed along the cylinder or in patches; it may, in turn, have a medullary layer filling the remainder of the space, thus forming a solid core; this is frequently poorly developed or lacking.

Another and less evident definition of the different types of thalli is "endogenous" and "exogenous". The former includes a certain number of the homoeomerous forms in which the green cells are thought of as the predominating and determining factor forming the thallus; in the latter, the hyphae take the lead in thalline development. This interpretation is based on the fact that the algal layer sometimes is highly gelatinous, thus dominating the thallus form, though there is a certain amount of gelatinization present in all lichens.

History

Before considering the disposition of the green layer and its relationship to the hyphal filaments in lichens, it is of interest to note some of the concepts that have evolved from investigations of this unusual plant combination. Lichens were first segregated as such by Tourneforte in 1694. Early lichenologists assumed for a long time that these plants were perfect and complete in themselves and not phases of algae, fungi, mosses and liverworts. According to their knowledge, it was held that the variously colored bodies in lichens arose probably from the hyphae, though some workers noted the similarity between the green and blue-green cells in these plants and certain free-living algae. Schwendener became convinced that it was more than a similarity, and on the basis of his anatomical studies stated that lichens were composed of two distinct portions, fungal and algal. The "compound organism" concept gradually became accepted and with it arose an explanation for the association as a case of symbiosis. Symbiosis with certain modifications is generally accepted, though the idea of autonomy still persists, as may be noted in the works of Elfving[8]. The problem of whether the fungal or algal symbiont ever becomes free in nature and is capable of living free during its whole life-period outside the symbiotic association is one which has been closely questioned. The autonomous conception may be anathema to most biologists, but it deserves certain considera-

[8] Bibliography reference numbers are given in the text only when there is more than one citation for an author.

tions that may lead to a clearer understanding of these unusual plant combinations.

Lichen Components. Every individual of a given lichen species, as far as is known, contains the same alga and fungus, giving to the whole plant a relatively constant form and structure. Occasionally, an abnormal development of the thallus, or cephalodia, contains an algal symbiont foreign to that found in other portions of the thallus. In the majority of lichens, Ascomycetes predominate as the fungal component; in three tropical genera, these are Basidiomycetes, while in a few others, Fungi Imperfecti are present. Thus, a primitive lichen, *Botrydina vulgaris,* has been described in which the fungal component appears to be a Hyphomycete of the Fungi Imperfecti (1). Mattirolo devised the term "Hymenolichen" for those lichens characterized by the association of an alga and a Basidiomycete; while the Ascolichen refers to the combination of ascomycetous fungi and algae.

The algal component may appear as a filamentous or non-filamentous type in the lichen thallus and has been referred, according to Schwendener's conception, to free-living forms. Thus, it may belong to the Chlorophyceae, most commonly to the genus *Cystococcus, Pleurococcus* or *Trentepohlia,* or to the Myxophyceae, most commonly to the genus *Nostoc, Gloeocapsa* or *Rivularia.*

Recent Investigations. Investigations on the type of gonidia present in the lichen thallus have contributed much concerning this association. Paulson (160–162) found that the gonidia of most lichens belong to a species of *Chlorella,* the cells of which do not divide vegetatively but reproduce by sporulation within the algal mother cells, much as in free *Chlorella* cells.

These views do not coincide with those of Warén and others interested in the behavior of the lichen thallus in culture media. Warén cultivated bright-green gonidia from 21 species of lichens, finding that they grow best on amino acid media. He classified the gonidia of most of our common lichens under the genus *Cystococcus* consisting of section *Eucystococcus* (*Protococcus*), in which there is vegetative division, and *Eleuterococcus* which shows autospore formation. Moreover, the gonidia from the different species show differences of form and color in the culture colonies, which led him to think that each lichen species had its own particular algal, perhaps not free-living symbiont. In this case it is

interesting to note that the algal symbiont of many lichens, as well as the fungal component, has been successfully cultured. Bioret, however, points out that in organisms so polymorphic as green algae, it is impossible to determine such specific or even racial aberrations. Warén further found that the gonidia in *Xanthoria parietina* (L.) Th. Fr. [= *Teloschistes parietinus* (L.) Norm.] from Finland differed from those of the same species collected in Holland.

Mameli (136), in her chemical studies of blue-green lichens, decided that in the lichen thallus the algal constituents suffered no important change except occasionally in increased size of the cells.

Variations in gonidia of lichens have been found by Linkola who cultivated *Nostoc* gonidia from eight different species of *Peltigera.* In *Peltigera malacea*[9], he thought that the variation may indicate some specific difference or only some particular physiological race. Chodat, in his studies of *Pleurococcus* gonidia of different lichen species, recognized them as being different from *Cystococcus* gonidia. During vegetative division the cells formed are easily confused with *Stichococcus,* explaining the view held by some lichenologists that at times gonidia of *Pleurococcus* type are modified by action of hyphae to *Stichococcus* forms.

Lichens have also been described in which the fungus and alga (217) were claimed to be associated with autotrophic bacteria (purple bacteria), but it has been proved conclusively that this is not so (207, 113); the purple color resulted from the presence of a lichenic acid secreted by the hyphae of the fungus. Cengia-Sambo (22) reports *Azotobacter* species in association with the fungal and algal component of a lichen.

Review of Theories. Schwendener, in presenting his hypothesis of the dual nature of lichens, believed this mutual relationship to be a state of parasitism of the fungus on the alga. If symbiosis is used in its generally accepted meaning as a harmless but intimate cellular association between at least two individuals belonging to different species, then it was Reinke who established the theory of lichen symbiosis. His term "consortium" was defined as two partners living peaceably together and working for the common good of the whole complex organism. Elenkin (50) found that

[9] Names of authorities will be omitted except in discussing synonymy.

destruction of algal cells goes on to a large extent at the lower side of the algal zone, his "necral zone". On this basis he proposed the theory of "endosaprophytism", indicating that the fungus ultimately devours the older algae. Smith (196), though accepting Elenkin's findings, preferred the symbiosis theory on the basis that such destruction of algal cells represents the normal wear and tear, which, in lichens, is compensated for by new growth from the gonidial region.

This has been well verified by studies on the relation between alga and fungus to determine the frequency of penetration of algal cells (163). There was not a single instance of penetration of algal partner by fungal hyphae in several common British species examined. They noted two forms of contact between the hypha and gonidium. In one, the gonidium was surrounded by loosely applied hyphae; in the other, the hypha was modified in shape so as to present a considerable surface to the gonidium. Many of the gonidia were dead, apparently because of "crowding together and lack of air", and the contents of such cells were absorbed by fungus hyphae, often without penetration of the wall. The relation between alga and fungus presents problems somewhat analogous to the mycorrhiza relationship in the Orchidaceae, which led Paulson and Hasting to suggest that each lichen may have to be taken on its own merits.

In contrast, Tobler (211) has recorded some interesting observations on this questionable relationship. He noted that at times the gonidia perished in the grip of hyphae where conditions favored the latter; but he also found examples of gonidia, perhaps favored by conditions of moisture, increasing enormously at the expense of the hyphae. He concludes that for the most part in the lichen thallus there is a constant balance of conditions between the two symbionts.

Bachmann (9), in the study of fungus galls of Cladoniaceae, affirms as a true symbiotic relationship what had been considered a form of parasitism. Mameli-Calvino (136) found occasional dead algae in the thallus, chiefly in the deeper layers where light is scarce.

Smith (196) further described lichens as being the most complete case of symbiosis. The balance is a delicate one but there is experimental proof for its existence. The Graphidaceae are

cited as an example of the striking degree to which the symbionts are mutually dependent. Until the algae and fungi come into contact, they lead a meager existence, but after the relationship has been established, each partner is seen to take on new vigor. Miss Smith points out that this true symbiosis or mutualism by which the fungus has acquired so much vigor, has given rise to a whole new class of plants with well defined peculiarities of structure and of cell products. The algal component has been less affected, but has gained in endurance against time, unfavorable conditions and, in some cases, in actual size of cells.

Nienburg and others suggested the term "helotism" or slavery, since the algae were apparently held by the intermingling hyphae of the fungi. Fry (72) considered this term untenable, maintaining that parasitism prevails though unaccompanied by any morphological distinction. Danilov speaks of a disease of the alga caused by the fungus, while Moreau (148) looked upon the lichen fungus as a gall structure caused by the exciting action of the alga. McWhorter advances as proof of the parasitic nature of lichen hyphae, the cases he observed in which mosses were destroyed by lichens. This was partly due to parasitism and partly due to smothering. This confirms Fink's (59) definition that "a lichen is a fungus which lives during all or a part of its life in parasitic relation with an algal host and also sustains relation with an organic and inorganic substratum". Martin compares a *Gymnosporangium* gall of a cedar tree to the lichen thallus. Both are specialized and characteristic structures. Both are the result of two organisms, host and parasite reacting upon each other. The only difference is in size. In the cedar apple the host is larger than the parasite; in the lichen thallus the parasite is larger.

Darbishire (36) concluded that the components of lichens cannot be treated separately, for as lichens they exist in a new, physiological tradition. The lichen has shaken off the habits, morphologically and structurally, of its parasitic or saprophytic ancestors. The total result is evident in the remarkable convergence in type of species, not necessarily related but growing under similar conditions.

Schwendener, while working on the histology of the lichen thallus, noted the great similarity in the structure of the algal cells and fungal filaments. The algal cells, but for the presence of

chlorophyll, had much in common with the colorless hyphae. More recently, Elfving, after careful study, suggested a genetic relationship in that gonidial cells, generally considered to be algal, are derived from colorless hyphae which are regarded as fungi. Strato observed *Peltigera canina* in nature and in transplanted cultures, in relation to growth and regeneration of the thallus. The results obtained by this author indicated that the algal host cells did not originate from the hyphae but were carried into regenerated areas by the developing hyphae, thus contradicting the views held by Minks and later affirmed by Elfving.

Reproduction

Asexual. Lichen reproduction may be sexual or asexual. In the latter, minute bunches of tangled hyphae with algal cells occur as soredia on the surface of the thallus and when blown loose by wind and deposited on the proper substratum, are capable of developing into thalli.

Herrmann has studied the development of soredia in Cladoniaceae and found that on a suitable substratum and under favorable conditions of moisture, light and temperature, the soredia develop into homogeneous thalli. First, the elongated, grasping or bridging hyphae grow out of the soredia, later followed by shorter ensnaring hyphae. This makes for a close alliance between the symbionts through entwining and enmeshing of the hyphae. The gonidia (*i.e.,* algae) divide, and at the same time intensification of color is brought about, perhaps, in response to stimulus of the lichen fungus. Division of free gonidia proceeds with a great reduction in the dimensions of the daughter gonidia which eventually die, as do the older enmeshed gonidia. The union of margins of neighboring soredial complexes by branching hyphae, and their fusion with one another, produces a morphological entity which is capable of repeating the life cycle. The possibility that soredia from different specimens come together accidentally, all contributing toward the final complete thallus, is suggested.

Production of soredia and fragmentation are probably the most important methods of reproductions in lichens, since a considerable number of foliose, as well as a few crustose and fruticose species, seldom produce apothecia and spores. Fragmentation was noticed

as a thin layer of wind-blown lichen fragments on the snow-crust above timberline on Mt. Washington (120). Rejuvenescence is quite common among species of *Cladonia* as the basal portion of the podetia die, and branching continues above.

Sexual (*Ascomycetes*). The sexual cycle of these plants is not clear, though the presence of sexual organs in some lichens has been well established. The male and female reproductive organs are known, respectively, as the "spermatogonia" and the "carpogonia". Spermatia are generally borne in the spermatogonia, though Bachmann (11) did not find this to be so in *Collema pulposum*. The carpogonium has a terminal branch or trichogyne through which the spermatia must travel to reach the female cell. The spermatia, being non-motile, are transported by mechanical means, that is, dew, rain or insects, and become lodged on the trichogyne with which they fuse (plasmogamy). The male nucleus wanders into the trichogyne and then backwards toward the ascogonial cell.

Moreau (149) points out that it is the custom to distinguish between two main types of Ascomycetes. One, like *Pyronema,* has a coenocytic ascogonium which copulates with a multinucleate antheridium. *Peltigera* and *Solorina* possess ascogonia of this type. Other Ascomycetes possess an ascogonium in the form of a winding thread with uninucleate cells. In such forms, fecundation is attributed to spermatia by the intermediation of a trichogyne, the extremity of which is extended above the surface of the thallus. This has been described by earlier workers and by Bachmann (11), working on species of Collemaceae.

In a later paper Moreau (150) reported that in *Collema nigrescens* the trichogyne is not a constant organ, as Stahl stated in 1877. In later stages of development the ascogonial cells grow, acquiring two rather than several nuclei. This makes room for branching hyphae with binucleate cells. The latter branch off, forming asci at their extremities. Spermatia are said not to take part in this development, but rather ascogonia give rise to ascogenous hyphae without having undergone fertilization. In the light of recent investigations of *Neurospora* by Backus one should not unqualifiedly accept Moreau's findings. The whole matter of spermatial fertilization in a great number of lichens is highly probable, though few have observed the process in its entirety.

The reproductive cell, or ascus, is contained in one or two types

of fruit bodies. In the Discomycete type the hymenium, or spore-producing layer, consists of asci intermixed with parallel packing hyphae, or paraphyses, and is fully exposed as a lining to a shallow, cup-shaped, fruit-body or apothecium. In the Pyrenomycete type, the asci are contained in a small flask-shaped structure, or perithecium, which opens outwardly by a minute opening or ostiole. The ripe ascus, usually containing eight spores, is a turgid, much elongated cell which forcibly discharges its ascospores into the air usually, as Werner (225) found in ascospores of crustose, fruticose and foliose lichens, from March to June. Hilitzer noted that in *Solorina saccata* spore discharge is dependent on the humidity of the thallus, especially of the lower cortical layer of apothecia which, when soaked, expands and exerts great pressure on the asci. Unlike most other Discomycetes, this lichen is dependent on heavy rains for its spore discharge. Production and liberation of its spores are continuous throughout the life of the apothecia.

Germination of Spores. On germinating, the ascospore is at first without the algae which it requires as gonidia, but when it comes into contact with its own particular alga, the fungus is stimulated to form a lichen thallus. The fungus is then able to grow independently of an organic substratum, as the green alga supplies the necessary organic food. The fungus absorbs water quickly, conserves it by reducing transpiration from the lichen surface, and thus furnishes its partner with moisture for a longer period than it would otherwise have at its disposal. In short, growth of the alga depends on the effort of the fungus which in turn is stimulated to greater activity by the metabolic action of the alga.

Determination of the exact relationship between the symbionts at this stage is of great interest. Cengia-Sambo (21) maintains that an oil, elaborated by the algal cells, is the first product of photosynthesis to be translocated to the hyphae of the fungal component. She further found (23) that in gonidia of Cyanophyceae the first product is glycogen; in the Chlorophyceae, it is an oil. Mameli-Calvino (137) could not affirm this, since in her research, starch was apparently the first substance produced, varying seasonally, disappearing in long periods of darkness, and present in and outside the gonidial cells. The latter conclusions agreed with those of Tobler (212) who further found that the fungal hyphae were able to excrete an enzyme capable of hydrolyzing this starch

in vitro. The starch external to the algae first disappeared when the plants were placed in the dark. In the lichen, the alga does not outgrow the fungus under normal conditions. Since the equilibrium between the algal and fungal components cannot always be maintained in the laboratory, we have a partial explanation for failure to secure successful synthesis of lichens under artificial conditions.

Thallus Formation. Werner (226) has observed the thallus formation of *Xanthoria parietina* and other species. The filaments, developing from the germinating spores, intertwine on finding free-living algae, forcing themselves between the algae and the substratum. As the alga increases in volume and divides, certain hyphal filaments separate the daughter gonidia, while others increase the colony by finding new algae. A cortical layer is formed around the gonidia and this enlarges so that the young colony takes on the appearance of a small thick "leaf". Gonidia become localized among the hyphae under the upper cortex and at the same time a medullary layer and lower cortex are formed, eventually producing elongated rhizoids at the periphery of the thallus. During the last phase the development of the cortex is oriented, and the hyphae of the medulla, by added growth, displace young gonidia so that they come to be located in the new parts of the cortex where algae are lacking. Thus it would appear that in the development of the lichen thallus, the fungal element is active whereas the algal unit is relatively passive.

Systematics

Although lichen algae have been referred to free-living genera, the fungal component, for the most part, cannot be compared to genera of fungi not found in lichens. Modification of the latter, as previously indicated, has reached a point where there is often little resemblance between them and the ancestral forms. It would seem that both fungi and algae should be classified separately. If attempted, this would involve a new classification and nomenclature of the lichen fungi. In a sense, this is being done, since the apothecia and spore characters of the fungal element are used extensively in subdividing the lichens into subclasses, orders and species, while the algal component contributes to the arrangement of families and genera. Elenkin (51) proposed a system based

on the essential types of fruiting bodies and habit of the lichen. On this basis he presents a chart showing the evolution of these plants and dividing them into normal families. Thomas proposed that the generic name of the lichen be provided with the ending "myces" and that the species name be placed in the genitive. Thus the lichen fungus of *Cladonia pyxidata* would be called *Cladoniamyces pyxidatae*. On the other hand, he would discard "gonidia" as a term for the lichen algae because of its vagueness.

Systematic lichenology is still in a hesitant stage. Authors with differing views constantly shift doubtful species from lichens to fungi and back. This is understandable when dealing with borderline species. For example, Mameli-Calvino (138) reports finding an epiphyllous Deuterolichen[10], *Chlorocyphella subtropica,* the fruiting body of which is a gymnocarpous receptacle inside of which conidia are produced. Though the perfect stage has not been reported, she unites it with the related species of *Chlorocyphella.* Martin regards lichens as fungi "eventually to be distributed among other fungi".

Magnusson (133) has criticized lichenologists for emphasizing one or two characters while equally important ones are ignored. Habits of growth and the presence of soredia or isidia are not, in general, sufficiently constant to be of great value in delimiting genera or species. $Ca(OCl)_2$, KOH, KI, HNO_3, paraphenylenediamine and other chemical reagents have been used to differentiate not only species, but varieties and a host of forms. Du Rietz (46) had earlier spoken against those who use chemical reactions as the basis of lichen systematics. Indication that the use of these reagents may lead to erroneous deductions was shown by Hesse (84) who reported that usnic acid was not a constant constituent of *Evernia prunastri,* since he had failed to find it in different samples of this lichen.

Gyelnik's use of unreliable morphological characters and chemicals in examining the Peltigeraceae has led to anything but clarity in that family. Scholander objected to Gyelnik's choice of variable chemical differences as diagnostic characters where morphological differences were lacking in founding species, varieties and forms. He states that: "Our knowledge of the physiology and chemistry of the lichens is insufficient, as is also the dependence on the sub-

[10] *i.e.,* Lichen Imperfectus.

stratum of their chemical substances. Neither do lichenologists generally know much of the chemical substances upon which they react. The result is that chemical characters can never be more than a help to distinguish between specimens which are morphologically defects or untypical. . . . By an assiduous use of KOH, $CaCl_2O_2$, Iodine . . . we could certainly increase immensely the number of species in genera".

Asahina's (6) studies on the color reaction of the lichen thallus to chemical reagents, based on innumerable analyses of the chemical nature of lichen acids and other substances, led him to conclude that chemical components are as important as morphological characters for purposes of lichen classification; such chemical reactions may be of value in specimens which are not well developed morphologically. In the Cladoniaceae, this practice has resulted in a multiplication of forms, consisting of slight variations, and resulting in no useful purpose. Yet Evans calls for a more exact usage of the terms "form" and "variety" in this already large family of lichens.

Literature

There is greater need for monographic studies, not only of families and genera, but of species. Zahlbruckner's (232) general treatment of the lichens of the world brings together a vast fund of information and synonymy which is available to the monographist. Such studies are necessary not only because of the present day uncertainty in regard to specific limits, but from a phytogeographical point of view which may well contribute facts on the distribution of phanerogams. An example is furnished by Darbishire (34), who in monographing the commercially important Roccellaceae revealed that the Old World species differed.

The more recent monographs on lichens include those of *Acarospora* (132), Cladoniaceae and Umbilicariaceae (68) and Physciaceae (130), as well as papers on the Usneaceae (153), on *Lecidea* of New York State (122) and on *Parmelia* (14).

Greater cooperation between lichenologists of the Old and New Worlds is fundamental; this would include an exchange not only of type specimens, reprints and ideas but of teachers and students for a better understanding of the many problems of lichenology. One such perplexing question is the conception of lichen species. For example, with reference to *Parmelia tubulosa* (Hag.) Bitter,

which has been found by the writer on Mt. Desert Island and occurs commonly in other areas, Degelius (42) states: "This species in the United States is too frequently overlooked. It is not mentioned at all in Fink's 'Flora' ". Dr. Berry evidently did not find it in the exsiccatae and collections studied, because it was probably not differentiated from closely allied species. Degelius (42) reports *Evernia mesomorpha* Nyl. as: "On the coast one of the most common lichens on coniferous trees . . .". With one exception, no reference has been made to the occurrence of these lichen species in recent contributions to American lichenology.

It is difficult for the individual student of lichens to secure a manual that will not only present him with a survey of the lichen flora of his country but will also have critical descriptions and comparisons with similar species in other countries. Smith's "British Lichens" and Fink's "The Lichen Flora of the United States" are two works available in English to the more advanced student. Detailed microscopic structure and critical comparative studies must be obtained from monographs or from papers in the various publications. More recently, Nearing has published the "Lichen Book" which is not intended for the specialist but because of its many figures and field characteristics, is a much needed guide to the American beginner in the study of lichenology.

Distribution

The problem of the geographical distribution of lichens is complicated by many factors and by lack of sufficient studies. The peculiar association of two different plants forming a whole, presents an element of uncertainty, for in reproduction only the fungal component is represented, and this must meet the particular alga with which it is associated. Since lichens are also able to perpetuate themselves asexually, and since they are adaptable and resistant to unfavorable conditions, they are found widely distributed.

Paleontological. Paleontology has contributed little to the problem of present day distribution. Fossil remains of lichens have not been found earlier than the Tertiary. The lichen thallus decomposes rapidly and when found, even in humus, is apt to be fragmentary. Yet Sernander (191) has noted remains in postglacial peat beds and on partly fossilized tree trunks. Deecke has found *Cladonia rangiferina* in loess of the upper Rhine region.

In general, we can suppose that where vascular floras have been known to exist, lichen floras may well have existed, in spite of the scarcity of fossil records. Correspondingly, lichens as well as phanerogams were probably pushed southward by the advancing ice of the last glacial period. Lynge (129), however, suggests that some may have existed in alpine refuges or along ice-free coast lines, noting that today some hardy arctic plants are found on nunataks.

Regional.

a. Arctic. In this respect, the investigations of the Scandinavians are of interest, for they have done considerable work on the Arctic element in lichen floras of temperate regions. Lynge (124) states that though microlichens are well represented in the Arctic, it is the macrolichens that appear to have the greatest distribution. In revising the genus *Rhizocarpon,* he (126) found that though there appeared to be a characteristic regional difference in the distribution of the group, only six were circumpolar. In a later paper, Lynge (128) states that many lichen genera grow at an unexpected elevation; that many of the commonest species have a wide and circumpolar distribution. In his studies of Novaya Zemlya (125), he records collecting 413 species of lichens as compared to 155 species of vascular plants. In a collection made in East Greenland, Lynge and Scholander found a lichen flora of only 102 species. He (129) concluded that the Arctic has a true lichen flora and not an extenuated southern flora, that this appears to be very uniform, and has been possible only because many of the species are very old in their present or adjacent areas, and because of their great conservatism.

b. Antarctic. Surveys of the Antarctic element in lichen floras of the South Temperate regions have revealed parallel examples. Du Rietz (47) found in the high mountains of New Zealand a great number of species identical with or at least nearly related to Arctic lichens. Some were not found at any other place in the southern hemisphere; others were noted in the Magellan region. This Magellanic distributional area is traced to the Boreal regions by a series of localities along the Andes. He records known lichens which have a distributional area connecting New Zealand with the Magellanic area through the Antarctic. This may account for the presence of arctic elements in the flora of

both South America and New Zealand. It also suggests the possibility of a migration route from Arctic to Antarctic by way of high mountain chains connecting these two regions during a period of uniform climate.

The New World and Russia alone have such north-south avenues which may provide evidence for this theory of distribution, but from a lichenologist's point of view, neither has been investigated.

Darbishire (35), comparing the Arctic and Antarctic lichen flora, pointed out their remarkable similarity in having in the species of both areas, a high percentage of fruticose lichens, which he considered evidence of their greater antiquity. Most of these are characterized by a very dark thallus. Hué, however, working on French Antarctic collections, found and described so many new plants that he concluded the lichen flora of Antarctica to be unrelated to that of any other region. Dodge, studying the lichens of the Byrd Expedition, reported that out of a possible 33 bipolar species, only one had been collected by the expedition, although 89 species in all were gathered of which 84 were described as new by the author. Lynge (131) has written a most interesting and exhaustive account of *Neuropogon sulphureus* (König) Elenk. [*Usnea sulphurea* Th. Fr.]. The genus is bipolar, being represented in the Arctic by one species and in the Antarctic by related species with intermediate localities in the high mountains of Ecuador and Peru.

Notwithstanding the fact that bipolar lichens have been found and that means for their distribution between these regions are available, it is quite possible that many lichen species have little capacity to migrate. This is brought out in collections made by a Finnish expedition in South America (171). Unless the continental drift theory of Wegener is accepted, it may be assumed that, for example, New Zealand and North American forms reached their present location along the narrow Cordilleran Chain since the rise of the Andes and the Rocky Mountains, which, considering the probable slight migration capacity of these plants, would appear unlikely. Yet the absence of bipolar species from tropical and occasionally from warm temperate zones is one of their best characteristics. For a more comprehensive study of the problem, see (48).

The idea that alpine vegetation might show an affinity with Arctic vegetation has occurred to many workers. In the United

States, Kiener lists 13 species of Peltigeraceae found in or close to the alpine zone on Long's Peak, Colorado, which he presented as such evidence. Llano advanced a similar view on the basis of a study of the lichen flora of Mt. Washington, New Hampshire. The genus *Cladonia* is well represented in the northern regions. Vainio enumerates 45 species of this genus in Finland. Savicz records 37 species in Kamtschatka, all part of the "circumpolar" group.

In *Acarospora,* Magnusson (132) found the genus to be cosmopolitan. These are lichens characteristically upland, some restricted to granitic or silicious substrata, but many found on calcareous rocks or earth. Their distribution was stated as follows: Europe, 100; Asia, 33; Africa, 39; North America, 71; South America, 19; Australia, 8; Antarctic, 3; Arctic Circumpolar, 1. Six were found common to North and South America and one common to the United States and the Antarctic.

c. Subarctic and North Temperate. Similarly, Suza records an arctic lichen, *Nephroma expallidum,* in Czechoslovakia and compares it with other arctic lichens in central Europe but not the Alps. Motyka (152), working at a lower level in the same region, revealed an astonishing similarity between the lichens of this area and those of the hilly region of the British Isles; the group *Cetraria* alone furnished 13 species common to both regions. On the other hand, Knowles has recorded tropical and subtropical species of lichens in southwest Ireland.

d. Tropical. The many climatic changes of the tropics have produced a greater abundance of species and individuals than is found in temperate and arctic regions. Northern species attain a larger size and certain families are especially abundant. The crustaceous groups, Thelotremaceae and Graphidaceae, are plentiful. Vainio, in a survey of Philippine lichens, has listed 635 species of which 178, or 28%, belonged to the tribe Graphideae, so that he concludes that this group reaches its maximum development in the tropics and will not be easily displaced from this position by additional discoveries.

Cengia-Sambo (24) has listed 60 species from Kenya and Tanganyika, noting that the lichen floras of these two areas show considerable similarity and relationship with the lichen flora of the Malayan Archipelago and the Philippine Islands. The genera

Parmelia and *Usnea* were best represented. Of a collection made in East Africa (25), 44 were characteristic of tropical or subtropical climates, 29 of temperate, and 14 were cosmopolitan in distribution.

It has already been noted that the Hymenolichens, including the genera *Cora, Corella* and *Dictyonema,* are exclusively lichens of eastern and western tropical regions.

It should be remembered that *Trentepohlia* is an abundant alga of the tropics which forms the gonidia of many of these lichen genera. However, Zahlbruckner (231), in collating all records of the lichen flora of Juan Fernandez Island, noted some interesting dissimilarities. Of the total number recorded, 25% had various blue-green algal symbionts, while 15% had *Trentepohlia* for a symbiont. In a study of the lichens of Samoa, he found a further falling off in lichens combined with *Trentepohlia,* while the blue-greens remained in the majority, that type of lichen being peculiarly a denizen of volcanic islands. This is of further interest because of the fact that blue-green algae appeared to be one of the first forms of plant life on Krakatoa and in the Katmai peninsula after volcanic action had decreased (79). Zahlbruckner (231) concluded that the lichen flora of Juan Fernandez Island was partly Chilean and partly sub-antarctic American in origin.

Relict Areas. From investigations of the distribution of lichen flora, studies of relict areas have developed. Torrey noted 15 species of lichens occurring southward in isolated areas at high altitudes in the United States. A more interesting case was that of *Parmelia tiliacea,* a coast lichen, which was found inland on relict marine areas which were once ornithocoprous sea cliffs and rocks of the Littorina period. This has been described by Sernander-Du Rietz in Sweden. Schindler finds *Teloschistes chrysophthalmus* and *Anaptychia leucomela* of the upper Rhine Valley to be relicts of forms which had a much wider oceanic distribution in Europe at one time. Degelius (41), in a most authoritative and comprehensive treatise of 22 oceanic lichen species of Europe, describes them as having a wide distribution, especially in the lower latitudes. Though in Scandinavia the oceanic lichens live mostly under optimal conditions and therefore cannot be considered as relicts, he concludes that their distribution in the rest of Europe would indicate them to be relicts of a Tertiary population which was broken up

and scattered during the last glacial epoch. The remaining species must have survived the epoch on some warm coast of southwest Europe. The history of this oceanic group is extremely complicated and their restriction cannot be due entirely to lack of effective means of distribution. Humidity, especially rainfall and fog, were locally important. Temperature was found to be less effective though mild winters at high altitudes play a significant part. Biotic factors were very important so that in favorable areas real oceanic communities were formed.

Since in East Africa Quaternary glaciation did not occur, Höeg chose Victoria Falls for a study of relict lichen epiphytes. He found neither a relict flora nor unusual types, even in the dense forest. The lichen vegetation proved to be poor in individuals and not rich in species. Lynge presents the many aspects of relict species in the "Dactylina Problem".

Origin and Evolution

The evolution of lichens is in many respects problematical. Church (28) saw little difference in structure between the Peltigeraceae and some fossil seaweeds, except that the lichen had lost assimilating cells which have been replaced, in function, by intrusive green or blue-green cells of algae. Miss Smith (196) aptly refers to these algae as "skinned seaweeds". In a later paper, Church (29) proceeds to trace the development of lichen fungus from seaweeds. After migrating from the sea, lack of nitrogen kept the plant impoverished, while the water problem tended to keep them small and restricted to short seasonal periods of growth. He concludes that lichens and fungi are evidently polyphyletic in origin.

Darbishire (37) objected to this theory, preferring to think of lichens as land plants entirely and descendants of simple fungi after their adaptation to parasitic and saprophytic land living. He bases these assumptions on the presence of air spaces or pores (188) in the thalli of lichens, which to him represents a long line of land ancestors, no matter how simple. In an earlier paper, Darbishire (36) stated that the evolutionary tendency of lichens seems to be along the line of increasing to the utmost the capacity for carbon assimilation. Galløe (73), in his studies of Danish lichens, concludes that they are derived from Oömycetes and that

changes have taken place as a result of psychic and immaterial processes: "I am most inclined to the view that the faculty present in the organism . . . is of a psychic immaterial nature". Fink (58) early held that part of the lichens were evolved from Discomycetes and part from Pyrenomycetes with such genera as *Peziza, Patellaria, Hysterographium, Phacidium, Chaetomium* and *Sordaria* among those which may be closely related to the ancestors of the lichens. In this respect he made a point of discontinuing to publish in the "Bryologist" in favor of the periodical "Mycologia". In a review of Smith's "Monograph of the British Lichens", Fink (61) commended the work highly but criticized the author for adhering to the concept of the duality of lichens. Again in a later review (62) of Smith's (198) "Lichens", he believed it unfortunate that the author did not follow the modern and logical interpretation that lichens are fungi using algae as hosts.

Physiology and Ecology

Metabolism. Experimental research on the physiology of these plants has revealed some interesting facts. Becquerel gradually dried in air and then in a desiccator, thalli of numerous lichens. These were exposed to a temperature of 268° C. for one to seven hours. On being returned to room temperature the lichens resumed normal metabolism. He further found that at low temperatures these plants are in a state of quiescence. He concludes that in arctic regions they resist cold, not because of snow protection but because of gradual dehydration by cold winds. Smyth, working with *Peltigera,* found that air-dried lichens retain 5% of water content and when desiccated over $CaCl_2$, 3 to 4%. The rate of respiration increases with temperature, as well as with a rise in water content, up to saturation point. The rate of assimilation increases with light intensity up to about 22,000 lux with the temperature between 10° C. and 35° C. Similarly, Ellée, experimenting with the same genus, found that assimilation of carbon dioxide by lichens was dependent upon their water content, the maximum being obtained at saturation. The younger part of the thallus showed better assimilation powers than the older parts. Measurements of light penetrating the lichen cortex indicated that about one quarter of the available light was able to pass through the gonidia layer when wet and only about one tenth when the

thallus was dry. Stålfelt, in a paper concerning gas excretion of lichens, found that lichens depended upon light and temperature for gas exchange, as with most plants; the total amount of light required for photosynthesis was high for the species studied. The optimum range of apparent photosynthesis was not sensitive to changes between 0° C. and 15° C. The ratio of apparent photosynthesis to dark respiration increases with decreasing temperatures. Thus, during winter, photosynthesis is intensive and without waste; during summer, photosynthesis is extensive with appreciable waste.

Neubauer found that the water content of lichens varies from 2 to 10% of dry weight on dry days to over 300% on rainy days. The respiration of lichens is two to three times as much when wet as when dry. Cuthbert, by the use of sensitive electric apparatus, found that *Teloschistes flavicans* is metabolically active with a water content as low as 0.4%. He proved experimentally its great facility to absorb vapor from the atmosphere surrounding it, and this together with the ability to survive with an exceedingly low water content, gives an explanation of the drought-resisting power of this plant. Bachmann (8) noted that crustaceous lichens absorbed more water, weight for weight, than foliose forms. On the other hand, they lost more water to begin with. Endolithic lichens were most retentive of water. He concludes that the presence of a layer of dead hyphae and gonidia is of importance in absorbing, retaining and storing water.

Rate of Growth. Rate of growth in lichens is somewhat debated. Cooper, in a 17-year study of phanerogam succession, incidentally noted no apparent change in lichen colonies in the Lake Superior region. Fink (60) carefully established quadrats and measured lichen growth of different species. He found it undesirable to draw any conclusions. Still, he noted that certain crustose lichens became established and produced thalli and apothecia in denuded areas in two to eight years. Foliose lichens increase in diameter from 0.3 to 3.5 cm. per year. *Cladonia* regenerates squamules in one or two years and podetia in three or four years, and these plants become established in succession in four to eight years. It appeared to him that on the studies of primary succession, full development of apothecia to the point where they assume their mature forms requires from four to eight years when the plants

are growing in their natural habitats. A much shorter time has been reported for development in cultures. The writer has studied specimens of *Teloschistes ramulosus* on *Thuja* twigs from Idaho, which had produced apothecia and spores in one year, as was ascertained from the fact that the thalli occurred on the previous year's leaves.

Effect of Substratum. Bachmann (10) found that some crustaceous lichens growing on bone did not draw any nutrition from the osseous tissue but that they benefited from the porosity of the substratum because of its great capacity of absorbing and retaining water, to the advantage of the lichen.

Mellor noted pitting by lichens on old church windows resulting from the mechanical action of the thallus. Fry (70) attempted to explain the mechanical force exhibited by lichens in the disintegration of rock. She found that films of gelatin, spread upon glass and dried, contract and tear away flakes of glass. Similar results were obtained when films of gelatin were dried upon smooth unweathered pieces of shale. The lichen thallus when wet is mucilaginous or gelatinous, and on contracting when dry, strips off thin sheets of stone in the same manner as drying gelatin. Rhizinae, rootlets and haptera of lichens appear to be mainly for attachment and of little significance as organs of absorption (198). Disintegration of rocks by lichens is therefore only partially due to the solvent effect of acids or excreted carbon dioxide; it results mainly from a mechanical action resulting from drying. Similarly, in studying the mechanical action of corticolous lichens (71), the bark is pulled up and broken by the shrinking of the thallus.

Ecological Factors. The number of important papers that have appeared on lichen ecology and habitat is indicative of the fact that lichens may be found everywhere except near the larger cities.

Frey and Ocksner account for the comparative richness of the lichen flora of central France by regarding it as the result of the greater uniformity of rock formations and forest conditions and partly as a result of the influence of oceanic climatic conditions. A rich growth of earth lichens was associated with a poor growth of epiphytes, and conversely. Lichen associations are best developed in luxuriant mats consisting of the fewest number of species. Exposure to sun, wind and available moisture are stressed as biotic factors. Davy de Virville pointed out that the lichen flora of the

coast of northern Portugal is similar to that of the Atlantic coast of France, but that lichens become less abundant toward the south because of a difference in the geologic constituents of the rocks and more intense solar radiation.

Nutritional Factors. Sernander (190) early recognized the influence of abundant nitrogen on the growth of certain lichens. He classified as "ornithocoprophilous" those forms which occur on rocks frequented by sea birds, and as "coniophilous" the forms found along roads where dung-laden dust was abundant. Degelius (40) found that the lichen flora of islands in the Kattegat was greatly influenced by the abundant bird life there. Lynge (128) emphasized the great importance of bird droppings on the arctic coast in the development of rich lichen flora. He conversely noted that the sparseness of lichens in northeast Greenland was due, not only to the dry climate during the time of vegetation, but to the absence of sea birds. Some lichens show a definite preference for calcium-bearing rocks and are recognized as being calciphilous. Among these, however, it has been found that some will grow on rocks having a slight trace of calcium but with (36%) magnesium oxide (179).

The work of some Europeans appears to affirm the presence of nitrogen-fixing bacteria in lichens. One such case of polysymbiosis has been noted in cephalodia of lichens (23). Iskina, using Winogradski's silica gel technique, reports finding nitrogen-fixing bacteria in *Cladonia rangiferina,* suggesting that these bacteria may have produced the "intragonidial wart-like swellings" previously described in these plants (33). The paper of Iskina throws some light on the nitrogen availability of those lichens inhabiting localities apparently lacking in nitrogenous substances. Zakharova reports that addition of "bios", extracted from yeast, stimulates the growth of these plants two to three times. He suggests that the presence of nitrogen-fixing bacteria within the thallus produces a similar "bios" which, with the carbohydrates evolved by the algal component, is utilized by the lichen fungus and influences growth and reproduction, controlling the stability of the plant.

Trümpener maintains that pH is an ecological factor of prime importance in the distribution of lichens, but he acknowledges that the nitrogen content of the substratum and air is important in certain species. He found nitrophilous lichens most abundant

at the base of trees and noted that the pH value tended to become lower, the higher they are taken on the tree.

Associations. Raup, in an investigation of the lichen flora of *Picea canadensis* (Mill.) B.S.P., found a distinct association. Crustose lichens occurred on the younger part of trees and branches; foliose, on older trunks, while a transitional region lay between the two. Important factors in the development of this association were age of the tree, roughness of bark, and exposure. Rassadina, from the structure of lichens distributed on tree trunks, concluded that their development is weaker on conifers than on deciduous trees. On deciduous trees, except birch and oak, he noted a difference in the grouping, depending on whether the bark was smooth or rough. He found that lichens usually occurred on the upper part of the trunk, regardless of the cardinal points. Haugh differs with Galløe (73) concerning development of lichens in beech forests. The latter stated that the poor lichen flora of beeches is due to deficiency of light in late winters and spring, resulting partly from the presence of dead leaves on the trees. The former concludes that optimum sites for growth of beech are poor in lichen growth because the trees grow rapidly, thereby shedding outer layers of bark often and at the same time forming dense stands which allow insufficient access of light. In ordinary forests, the slower growing trees carry more lichens.

Plitt (168) shows that the lichens of Mt. Desert Island and Blue Mountain indicate a definite competition resulting in a noticeable succession of crustose and foliose forms followed by fruticose species. The exact species to succeed is determined by the closeness of the attachment to the substratum, the less closely attached ones being able to overgrow the others. Moreau (151) observed the same thing in France, noting the more abundant crustose species on wind-exposed surfaces.

Lichens are plants characteristic of exposed, windswept and unfavorable habitats, prominent in alpine and arctic areas; they are equally at home on cold, foggy coasts and on trees of the tropics; along lake shores, in brooks, between tide marks, while one species has been secured from the Baikal Sea (92). They are considered pioneers in the scheme of plant succession, though they may actually form a permanent stage and not just a step in an ecological sense. Their reputation as rock destroyers and formers of soil has been considerably exaggerated.

Under such conditions of distribution and habitat, lichens show many converging forms influenced, no doubt, by external factors as well as by individual variation. These factors and variations are so insufficiently understood at present that detailed splitting into habitat groups can do little but obscure the general geographical trends. For present purposes, the older usage of the terms "crustaceous", "foliose" and "fruticose", with formations named after the dominant form, would do much to simplify the problem.

CHEMISTRY OF LICHENS

In the past 50 years about 200 compounds have been extracted from various species of lichens, mostly by German, Japanese and Italian workers. These compounds have not been found in any other group of plants and are thought to be due to the peculiar morphological association in these plants. The chemical constitution of about 12 of these compounds is known, although the empirical formula of most of them have been published. With few exceptions, all contain oxygen and are acid or neutral.

Our knowledge of the elementary chemical composition of lichen products and of the constitution of the chemical substances in them is comparatively new; as a result of the later investigations of Zopf and Hesse, we have a better understanding of them. As early as 1808, Berzelius (15) discovered that many species of lichens on extraction with hot water yielded a gelatinizing substance which he named "Flechtenstärke" (lichenin); later investigators have shown this to be not a single substance but a number of related carbohydrates. The names of some of these substances are indicative of the species from which they have been extracted, as "evernin" from *Evernia prunastri* and "usnin" from *Usnea barbata*. Of late years, Karrer and his collaborators have characterized lichenin as the "reserve cellulose" of lichens and have found it in the seeds of various higher plants. Reference will be made later to the action of ferments, especially lichenase, on lichenin in lichens used as food by snails. Lichen starch (lichenin) is said by Haas and Hill to be chemically, but not physically, identical with amylose of starch grain. It is also said to be closely related to cellulose, having similar optical and chemical properties as cotton.

The constitution and properties of some of these substances (evernic, usnic, obtusatic, and olivetoric acid, also atranorine)

have been found to be related. Some, as rangiformic acid, appear to resemble fatty acids; others have been named "depsides" by Fischer who found their chain compounds analogous to peptides produced by linking together similar hydroxyl groups. Tanning substances are an example of this category of compounds, thus suggesting Fischer's use of the term "depside" from the Greek "to tan". Naturally occurring depsides are found chiefly in lichens, *i.e.*, lichen acids.

Employment of lichens as raw materials in pastries, confectionery, food, and in the production of alcohol depends largely on the properties of lichenin. The presence of a certain number of phenols, acid-phenols, and acid-phenol-ethers together with other substances in extracts of *Evernia prunastri* and other lichens, forms the basis of their use in perfumery and cosmetics. The tinctorial properties of lichens, long used in dye industries, are for the most part derivatives of orcinols in species of *Roccella*. In 1934, Asahina reviewed the progress of the chemistry of lichen acids from the time of Zopf and Hesse. Since this represents the most recent summary, it has been referred to in this study.

The chemical substances never occur in great quantities. Their detection involves fine, complex techniques; production of lichen substances for commercial use is rather limited and specialized. At present, this information is most interesting from an academic point of view, yet basic to a more complete understanding of the economic possibilities of the class Lichenes.

ECONOMIC USES OF LICHENS

Food for Invertebrates

Smith (198) has secured from the literature a large number of records of invertebrates known to feed partly or wholly on lichens. This includes not only mites, caterpillars, earwigs and black termites, but also snails and slugs. These animals appear to feed on all but the most gelatinous ones.

More recently Schmid has observed the snails *Chondrina avenacea* Brug. and *Pyramidula rupestris* Drop. feeding on the endolithic lichens, *Verrucaria* and *Protoblastenia*. They obtained the lichen by corrosion and ingestion of the rock surface, grazing mainly on the thallus and apothecia. Excrement from these snails contained fragments of calcium carbonate and green algae cells,

while the hyphae and dead algal cells were apparently digested. All this is of interest, since there is a widely current assumption that lichens are remarkably well protected against attacks from animals by reason of acid substances produced by them. Not a few "new" species of lichens have been the result of insect and snail ravages, further modified by regeneration on the part of the plant (181).

Experiments have shown that snails will feed on potatoes covered with cetraric acid and on acids, rhizocarpic and pinastrinic, poisonous to other animals, but will not feed on vulpinic, recognized as poisonous to vertebrates (198). Crystals of the acid pass through the alimentary canal unchanged and are deposited in slime-covered masses in the feces. Bitter-tasting lichens, treated by a (198) soda method to extract the acids, were acceptable to many animals in preference to moistened, fresh lichens. Dry hard lichens are rarely attacked, while gelatinous ones offer a mechanical protection that gives them almost complete immunity from small animals. Algae are preferred in all cases, but when not obtainable the gonidia, *i.e.,* algal layers in lichen thallus, are resorted to for food. Hué goes so far as to state that the abundance of lichens in arctic regions results from the comparative absence there of snails and insects.

Lichens Used as Fodder

Non-grassy Ranges. North of tree line and above timber line there exist large irregular areas consisting of many square miles that may be classified as non-grassy range feed, covered with carpet-lichens serving in the capacity of grasses. The most continuous such areas are in the sub-arctic but these also extend into the north temperate zone and cover parts of Greenland, Iceland, Scandinavia, Siberia, Alaska, the Northwest Territories of Canada, and Labrador, as well as the many islands of the Arctic Ocean. In the Antarctic, lichens, though present, are not strongly developed because of unfavorable factors. Similarly, scattered and isolated non-grassy range lands are also present above timber line and well down into the timber of mountain sides.

The most useful species (198) are the so-called Reindeer Lichens: *Cladonia rangiferina, Cladonia alpestris* and *Cladonia sylvatica.* Zopf (198) states that the last is refused by reindeer. Included with this group are *Cetraria islandica, Cetraria crispa*

and *Cetraria Delisei*. . .Probably others, as *Stereocaulon* spp. and *Alectoria* spp., are accidentally eaten, since they are to be found together. The Cladoniaceae are the most important, since they grow in carpet-like masses to a height of six or more inches. They appear to be less dependent on the substratum and grow equally well on all suitable areas, especially after fire, competing with and preventing development of certain seedlings. They may be covered for long periods by snow. Those animals that feed on them are accustomed to dig through this cover to obtain them. They support the reindeer which, in turn, make possible the existence of Lapplanders in northern Scandinavia. They are grazed by herds of caribou, wood buffalo, musk-ox and other animals in Arctic and Boreal America and provide an existence not only to the Eskimo and northern Indians, but to the white fur-hunters and traders. With the introduction of reindeer for the more stable support of Eskimos in the North, the value of these non-grassy ranges takes on new significance. A report of 1929 (200) by the United States Department of Agriculture in Alaska, where reindeer had been imported some years ago, states that there already is danger of over-grazing in this area. This is a problem that the Scandinavians have met with some success.

Use of lichens as fodder has always received attention in times of forage scarcity, while in some parts of the world they are regularly used for this purpose. Investigations concerning their food value and growing habits as well as the feeding habits of reindeer have been made at various times (121, 96). Lynge (123) presents the following interesting accounts.

In 1916, the large lichen fields of Finmarken maintained 100,000 head of reindeer which resulted in a serious over-grazing problem. The smaller fields in the Norwegian Provinces supported 50,000 of these animals. In order to remedy this condition, regulations prohibiting reindeer pasturing about Ravnastuen, Finmarken, had to be enforced for some time until good growth was reestablished. Under conditions of unrestricted grazing, lichen vegetation may be seriously altered, while mere trampling of large herds in small areas will also destroy these plants. In fields of *Cladonia alpestris*, *Stereocaulon paschale* comes in, producing full grown thalli in five to six years, after which *Cladonia alpestris* again becomes dominant.

In Lynge's account there is a list of Lapponian lichen terms

contributed by Kristian Nissen, indicative of some of the peculiarities connected with reindeer husbandry. The Lapplanders, because of their association with these animals, have learned not to confuse mosses with lichens, since reindeer do not feed on the former though they will apparently take all accessible lichens. Lichen feed is classified under three headings. "Jaegel" refers to field lichens and includes the Cladoneae, Cetrareae and Stereocauloneae on which they fatten; "Gadna" or the Parmeleae and Gyrophoreae which occur on stones and trees and are eaten if no other food is available; while "Lappo" are the beard forms as Allectoreae and Usneae for which the animals have great fondness, and though these will support life, the reindeer do not fatten on them. The herders also recognize the pasture cycle after fire with its successive lichen formations. In all cases the reindeer prefer younger parts of the plants.

The relative abundance of these economic lichens would be best stated as "generally common", for solid areas of any one species is the exception rather than the rule. *Cetraria islandica* in average areas yields approximately 700 kilograms of air-dried "moss" per square kilometer. *Cladonia alpestris* gives higher yields, the richest fields being between Nordre Osterdalen and Finmarken with miles of lichen fields extending from the Swedish frontier to the Glommen valley. Selected areas here have produced 1400–1500 kilos per 1000 square meters.

Harvesting is performed by hand or implements. Among the Lapplanders, the work is done by women. Rakes or broad forks are used by men to clear the lichen vegetation away in broad strips, resulting in higher yields. The Lapponian method is more conserving and based on cheaper labor, since only a quarter of the quantity growing is gathered, leaving enough for regeneration. The Norwegian method takes up two-thirds of the amount available; this varies considerably with the person and the field. Dry "moss" is brittle and therefore most economically harvested when having a water content of 40–70%. As the plant is gathered, it is piled in small heaps (40–50 centimeters high) with a branch of birch in the center for a handle. The many small heaps are then brought together to form larger bundles. These are then taken to the drying house in sledge loads of from 300–600 kilograms, the bundles being gathered in the winter. Transportation

costs are high. "Moss" presses are little used because of their expense and weight.

In the drying house the crop is spread out on the floor of a warm ventilated room, so that it does not lose too much weight, and is stored with a water content of from 14–15%.

A farmer having 10 cows and some sheep and goats uses yearly 60 sledge loads of lichens for his stock. This implies a need of 4,800–18,000 square meters of well covered lichen fields a year. Since these plants require 30 years to regenerate a marketable stand, a farmer must have access to 150,000 to 560,000 square meters of land. This land must preferably be mountain land, since forest areas contain pine needles. However, few farmers give so much lichen fodder to their cattle, actual amounts depending on the amount of grass available. In "moss" districts, three to five sledge loads are collected per cow.

As an additional food for domestic animals, especially swine, lichens are of value, and Lynge recommends greater use of svinamose (swine-moss) for these animals. Jacobj found that young pigs throve better on a combination of reindeer moss and ordinary feed than with the latter alone. He also fed rabbits and hares with *Evernia prunastri,* after extracting the acids, with satisfactory results. Icelanders feed *Cetraria islandica* to their cattle and ponies. It has also been reported good for oxen (228), while the richness of the milk of the small cows of northern Scandinavia is attributed to this food (100).

Nutritional Studies. The nutritive value of these non-grassy range feeds apparently lies in their high lichenin (lichen starch) content and in the fact that they are less bitter than most lichens. Hesse (86) worked out a comparison of their sugar content with that of potatoes and found that for *Cetraria islandica* the proportion was 1 of potatoes to 3.35 of lichen; for *Cladonia rangiferina,* 1 : 2.5. The former has been found to yield 61% carbohydrates and other products of its hemicelluloses. The bitter principle, due to the presence of lichen acids in even the mildest of these plants, must however be removed in order to make the fodder palatable to animals. This is done by soaking them in water for 24 hours or by addition of potassium carbonate to the water for quicker action. Sometimes the lichen is mixed in hot water with straw and salt before being fed to cattle. It is this

action which removes the fumarprotocetraric and other acids from the plants. Use of lichen fodder goes back into antiquity, as indicated by prehistoric remains found near Lake Constance in Switzerland (198).

Lichens Used as Food by Man

History of Human Use. From the earliest times the food of man has included lichens, sometimes as a delicacy, but more often as the last resort in the face of starvation. In either case, they are of little importance commercially, though Swartz quotes Hanstien, chief lecturer in the Agricultural School at Aas, Norway, who prophesied that lichens were destined to become the great popular food for the masses, because of their cheapness and nutritive value. But the bitter principle of these plants gives them an unpleasant flavor, is difficult to remove, and exerts an irritating effect upon the digestive tract of man, causing inflammation. More recent studies in the field of experimental physiology have revealed some nutritional facts about these foodstuffs.

Cetraria islandica probably rates first as human lichen food. It was occasionally gathered commercially in the Scandinavian countries and in Iceland and sold on the market as Iceland Moss. Preparation includes removal of foreign material and soaking; then it is dried and powdered. It is made ready for human consumption by boiling as a broth which on cooling sets as a jelly. Milk is added and in this form the lichen is the basis of various light and easily digested soups and other delicacies said to be of value for dyspeptics. It may be made into bread, porridge or gruel. Schneider says of this "moss": "Inhabitants of Iceland, Norway and Sweden mix this with various cereals and mashed potatoes from which an uncommonly healthful bread was prepared". Lynge (196) quotes a tradition "that there was no starvation at Modun in 1812 as long as there was bread-moss (brødmose) left in the forest". It was also mixed with ship's flour, making the bread less friable or less subject to weevil attack. In northern Finland, in times of famine, reindeer moss and rye were made into a bread having a taste like wheat bran but leaving a sense of heat on the tongue. "Tripe de Roche" or Rock Tripe was so named by the French Courreur de Bois of Boreal America who used it in periods of emergency. Franklin (215) recorded it in his diary as the main course of many a meal. This "Tripe"

is usually one of the Umbilicareae which must be treated by boiling or soaking before being eaten. The American Indian's knowledge of wild food plants included use of *Alectoria jubata* (230).

The biblical manna of the Israelites may have been *Lecanora esculenta* (198) which is still eaten by desert tribes, being mixed with meal to one-third of its weight. This lichen grows in the mountainous regions and is blown by high winds down into the lowlands where the thalli form little hummocks in the valley. As late as 1891 (Pharm. Jour.) there was an abundant fall of this "manna" in Turkey. The ancient Egyptians made bread, using *Evernia prunastri* and *Evernia furfuracea* (101). There is still some importation of these lichens from Europe as fermentative agents; Forstal in the 19th century saw several consignments from Islands of Archipelago for Alexandria (169). In India (198) a *Parmelia* species is used as food, generally a curry powder, and medicinally; while in Japan *Umbilicaria esculenta* is considered a delicacy and sold as "iwa-take" or "rock mushroom". Collecting places are scarce and difficult of access so that the market price is very high (105). In France, lichens are used in the manufacture of chocolates and in the pastry business, largely because of the properties of lichenin (158).

Nutritional Studies. Scientific investigations as to the digestibility of lichens and the behavior of lichen substances in the body have been too few, but the evidence at hand does not agree entirely with the fact that these plants are used extensively as food stuffs. Analyses have shown that they contain a variety of carbohydrates of which polysaccharides are the most common, giving rise, on hydration, to several sugars, some cellulose, chitosan, glucosamine and inulin. Of these the only compounds directly available in intermediate metabolism are the simple monosaccharides, *i.e.,* six-carbon sugars. Polysaccharides apparently need to be split into "physiological" sugars before they become available in the body. Ullander and Tollens noted a difference in the occurrence of characteristic carbohydrates in various lichens examined, though they all contained some lichenin. Thinking that the substances in *Cetraria islandica* and *Cetraria nivalis* were similar, Poulsson made a bread from these two species to determine their use in diabetes mellitus. Though 46–49% of the carbohydrates of the former species was digested, the latter species caused such intes-

tinal disturbances that the experiment had to be discontinued. Brown failed to induce glycogen formation in rabbits by feeding them lichenin obtained from Iceland Moss. Ordinarily neither emylytic enzymes nor hydrochloric acid (0.3–0.5%) have any noticeable effect on lichenin, while iso-lichenin is, at most, converted into a dextrin-like form without producing sugar; the action of bacteria yields acetic, proprionic, butyric and lactic acids (102).

More recently Wallerstein fed mice white bread, later replacing it with lichenin, and showed the latter to be 53–64% utilized. Similarly, Shimizer (193), in determining the influence of some polysaccharides on the protein balance of a dog, found that they were digestible and available foodstuffs in the alimentary canal; though how, he did not state. Later (194) he digested polysaccharides *in vitro,* using extracts of macerated intestine and pancreas in an 0.8% NaCl solution but found no monosaccharides. He took this as evidence that there are no enzymes in the digestive system of mammals capable of splitting inulin, lichenin or hemicelluloses. On determining the action of fecal material and fermentative bacteria on these substances, Shimizer and Tonihide (195) concluded that they are split into sugars by the bacteria in the digestive tract of mammals and can then be absorbed.

It has been assumed in the past that the presence of the enzyme lichenase in the stomach contents of the ox and pig probably enable these animals to convert lichenin into the more digestible sugars (103). The action of snail lichenase on lichenin *in vitro* has been found to produce cellobiose and lichosan, an anhydride of glucose similar to cellosan, a product of cellulose. Messerle states that the livers of snails contain much lichenase which converts cellulose to sugar. Jewell and Lewis had found this to be true of many invertebrates, suggesting that the ability to hydrolize lichenin may be characteristic of invertebrates only.

Swartz questions the value of algae and lichens as sources of energy in nutrition. Oshima suggests that they may be valuable for their inorganic salts, while Prausnitz calls them "faeces-forming foods" in that they stimulate intestinal activities. Most of Swartz's studies were on the algae, yet she was able to draw certain conclusions concerning those chemical substances common to both plants. These were:

a) Nutritive studies of lichens would indicate that as energy

producers their value is not appreciable. Yet the fact remains that certain animals do feed upon them and thus sustain themselves in regions where energy and high body heat are prerequisites to life. (The order of resistance of hemicelluloses to bacterial action was noted by Saiki—as galactans, pentosans, levulans and mannans —and herbivores were found to do better on pentosans, not at all on mannans.) The assumption follows that our understanding of the value of lichens as fodder is still incomplete, though ruminants are apparently more effective users of hemicellulose than other animals.

b) Aerobic and anaerobic bacteria, not enzymes, are responsible for conversion of hemicelluloses into sugars. The amount available to the animal system is extremely diverse, depending on the animal and the lichen; in dogs the ratio of digestibility of pentosans varied from 25–75.

Vitamin Studies. Nutritionists have assayed lichens from the vitamin point of view. Blix and Rydin found that *Cladonia rangiferina* contains some ergosterol, more than most lichens, but the content is low in comparison to yeasts and molds. This is a substance similar in composition to cholesterol. This same species collected in Upsala in August and September showed only traces of Vitamin D.

Feeding experiments with rats failed to show Vitamin B or G in either of two samples of short and tall lichens obtained in Alaska (54). Short-growth lichens gave more Vitamin A and less Vitamin D than tall-growth types. Short-growth types appeared more palatable to rats. Unfortunately, in this experiment the names of the lichens used were not indicated, so that this evidence is only of the most general interest. Bourne and Allen, using acetic acid-silver nitrate reagent for Vitamin C, obtained a positive test in lichens.

Medicines and Poisons Derived from Lichens

The name "lichen" is a word of Greek origin meaning "leprous", used by Theophrastus in his "History of Plants" to signify a superficial growth on the bark of olive trees. The term originally applied to hepatics. Dioscorides applied it to true lichens on account of their resemblance to the cutaneous disease for which they were supposed to be specific.

History. Medicinally these plants can be traced back to a very remote age. *Evernia furfuracea* has been found in an Egyptian vase from the 18th Dynasty (1700–1600 B.C.). It is still sold in Egypt with *Cetraria islandica* as foreign drugs, being imported from Europe (198).

In the 15th century A.D. there was throughout Europe a constant attempt to follow the guidance of nature in the study and treatment of disease. It was believed that Providence had scattered here and there on plants "signatures" of resemblances more or less vague to parts of the human body, or to the diseases to which man is subject, thus indicating the appropriate specific. This era was the climax of the commercial importance of these plants, for never before or since have they played such a unique role in the world of economic plants.

The long filaments of *Usnea barbata* were used to strengthen the hair, though Hippocrates prescribed it for uterine ailments (114). The natives of the Malay Peninsula (66) still use this plant for colds and strengthening after confinement. *Lobaria pulmonaria* was the suitable remedy for lung troubles. Boerhaave (*Aphor. comment. de Van Swieten*) regarded it as an excitant, tonic and astringent and hence recommended it for hemorrhages and asthma. *Xanthoria parietina,* being a yellow lichen, was supposed to cure jaundice, while *Peltigera aphthosa,* the thallus of which is dotted with small wart-like tubercles, was recommended for children who suffered from "thrush". Other species of *Evernia, Peltigera, Parmelia, Cladonia, Roccella* and *Pertusaria* were used to control fevers, diarrhea, infections, skin diseases, epilepsy, convulsions and as purgatives. *Pertusaria communis* was especially interesting in that it was used to cure intermittent fever, having less action on women than men (114). *Peltigera canina,* as a cure for hydrophobia, was sold by a famous Dr. Mead as the celebrated "Pulvus antilyssus" (Dillenius 1741), while the so-called drug "Lichen quercinus virdes" consisted mostly of *Evernia prunastri, Evernia furfuracea* and *Parmelia physodes* (189). The doctrine reached the height of absurdity in the extravagant value set on a lichen found growing on human skulls, "Mucus cranii humani". This skull lichen, *Parmelia saxatilis* (*Physcia?*), as a cure for epilepsy, fetched its weight in gold.

Luyken, in his "Historia Lichenum in Genere", Göttingen 1809,

gives a long list of medicinal "Lichenes, quorum usus obsoletus est". Yet as late as 1927 (219) there appeared in the Paris Medical Bulletin a discussion of the probability of true lichens being the cause of some skin diseases, with notes on therapeutic methods to be employed if laboratory findings should corroborate this. Plitt (167) recommended more emphasis on the study of lichenology to pharmacognosis, venturing the opinion that the medical virtues of bark drugs may be affected by the lichens growing on them.

Reference has already been made to lichenin and the many acid compounds present in lichens which give them a bitter and astringent taste. Some of them may have been of value as curative herbs, but all with the exception of one have been replaced by more effective modern drugs.

"Iceland moss" was given an important place in medicine by Linnaeus in 1737. It has been used in chronic affections as an emollient and tonic, and it would indeed have been a "Divine gift to man" had it lived up to all its prescriptions (31). Today it is used as a substitute for salve bases in the preparation of emulsions, the reduction of the bitter taste in certain drugs, as a laxative and as a culture medium for bacteria (166).

Physiology. The physiological action of the cetraric acid of "Iceland moss" has been studied by Kobert. It has no poisonous effect either when injected into the blood or when taken into the stomach of small animals. Small doses induce peristaltic movements in the intestines. Large doses may injure an animal, but if given as free cetraric acid, it passes through the stomach unchanged to become slowly and completely dissolved in the intestine. The mucous membrane of the intestine of animals that had been treated with an overdose, was found to be richer in blood, so that Kobert assumed that cetraric acid would be useful in assisting digestion. A more reasonable explanation might be that the lichen acid irritated the sensitive mucous membrane and produced inflammation. In this sense, cetraric acid would hardly serve as an aid to digestion. It has also been used as a nerve excitant.

It is interesting in this respect to note that Asahina and Fujikawa, in 1932, extracted (by means of acetone) from *Ramalina calicaris d*-usninic, evernic and obtusatic acids. The last named acid was the same as Makao obtained from the Manchurian drug Shi-hoa.

Lichens with few exceptions are non-poisonous, though their acid substances have proven extremely irritating when taken internally. The supposedly poisonous exceptions are the species *Evernia vulpina* and *Cetraria pinastri.* The former contains vulpinic acid in the cortical cells, the crystals of which are lemon yellow in the mass. The latter species and *Cetraria juniperina* (111) produce pinastrinic acid in the hyphae of the medulla and the crystals are orange or golden-yellow. These have been used in northern countries to poison wolves (198). Carcasses are stuffed with lichen and powdered glass, the wounds caused by the glass rendering the internal organs extremely sensitive to the action of the lichen acids. It would appear that the ground glass was sufficient to cause the death of the animals.

More recently a report of the Wyoming Agricultural Experimental Station (229) on a study of the presence of selenium in soil and various plants states that *Parmelia molliuscula* contains this poisonous salt in sufficient quantities to affect sheep and cattle. It produces a lack of coordination of the hind limbs; in severe cases the animals are unable to move either hind or fore legs. Other cases of lichens containing such elements include beryllium (57) in *Parmelia saxatilis* and *Xanthoria parietina,* chlorine (111) in *Evernia furfuracea.*

The physiology of lichen poisons has been studied (112, 156). Experiments on cold and warm blooded animals have proven fatal, the cat being the most sensitive of mammals and the hedgehog the least sensitive of those used in the tests.

Industrial Uses of Lichens

Brewing and Distilling. Use of lichens instead of hops for the brewing of beer is mentioned as occurring in Russia (114) and Siberia (215). Its use appeared to be confined to one or more monasteries in Europe which had a reputation of serving bitter but highly intoxicating beer to the traveler. Tuckerman further describes a by-product of *Lobaria pulmonaria,* "a yellow, nearly insipid mucilage which may be eaten with salt".

Alcohol production from lichens is an old art, more recently replaced by increased cultivation of potatoes and importation of sugar, better adapted to fermentation. Preparation of spirits from lichens was recommended in 1870 (201) as a means of saving

grain otherwise diverted into alcohol production. This same writer claimed that 20 pounds of lichen would yield five liters of 50% alcohol. In 1893 (82) the manufacture of brandy from lichen alcohol had become a large industry in Sweden, though by 1884, as a result of local exhaustion of the plant, the industry languished. Arendt, in 1872, reported that this originally Swedish discovery was being applied in the Russian Provinces of Archangel, Pskow, Novgorod, *etc.*, and that various distillers exhibited samples of lichen spirits at the Russian Industrial Exhibition in Moscow, which were highly approved by the French and English visitors. The industry was a lucrative one in the northern provinces of Russia, yielding a net revenue of from 40–100%.

Lichens may vary in the amount of carbohydrates (lichenin) present. *Cetraria islandica* and *Cladonia rangiferina* have been found to yield up to 66% of polysaccharides which are readily hydrolyzed to glucose and then almost completely fermented to alcohol. Besides sugars capable of fermentation, lichen acids up to 11% of air-dried substance may be present. These acids (cetraric) as well as sodium chloride have been found to retard the process.

Experiments (54) with *Cladonia rangiferina* have shown a total yield of 54.5% sugar which on fermentation produced 176–282 cc of alcohol per kilogram of the plant. Maximum returns of alcohol were obtained by steaming the lichens one hour under three atmospheres pressure, adding 2.5% of 25% hydrochloric acid, resteaming for the same period of time and pressure, finally neutralizing the product. Subsequent growth of yeast was normal though fermentation may be accelerated by addition of H_3PO_4. An interesting modification of this procedure through addition of three parts by weight of sulfuric acid and one part by weight of nitric acid at room temperature, gave a pentanitrate similar to cellulose nitrate which, on gelatinizing with a solvent, produced a substance resembling horn (174).

Tanning and Dyeing. The tanning quality of lichens is due to an astringent property peculiar to some species (116). *Cetraria islandica* and *Lobaria pulmonaria* are most used and though not occurring in quantities sufficiently large to warrant industrial application, are locally employed on a small scale. "Many crustaceous lichens contain oxalic acid in greater or less abundance; according to M. Braconnet, this occurs in the bitter *Variolaria* (*Pertusaria*

sp.) in such quantities that 100 parts yielded 18 of lime, combined with 29.4 of oxalic acid; and the lichen is now employed in France in the manufacture of the acid on a very extensive scale" (215).

The development of synthetic aniline dyes has largely replaced many common vegetable dyes. Of these, the lichen dyes were renowned for their high quality and color, some of which are still popular in rural districts of Great Britain and the Western Isles, Iceland, Scandinavia, France, Germany and the United States. The writings in 1787 of Amoreux, of Hoffmann who included in his "Commentatio de Vario Lichenum Usu" 77 samples with color names as used by the French "tienturies" of his day, and of Willemet reflect the part these plants played in the economics of the period. Westring in 1792 distinguished between lichen dyes which impart color to pure water (essential pigments) and those requiring certain treatment to yield color (preparable pigments). Lebail in 1853, Lindsay in 1854 and others had classified them according to the color produced, recognizing that color varied with treatment and that the hue of the plant *in situ* was no indication of the dye it might yield. The system followed by the writer is of a more general nature, based on records in the literature examined, some of which may be doubtful. Where possible, the nomenclature has been brought up-to-date (Appendix).

a) *History.* Of all the lichen dyes used by man, none has attained greater historical and commercial importance than those of the Roccellaceae, variously known to the English as Orchella Moss or Weed, Archil or Orchil paste or liquid, to the French as Orseille, and to the Germans as Persis. Theophrastus and Pliny both knew of the dye, while the Bible refers the origin to the "Isles of Elisha". During the Middle Ages the art of making dye from *Roccellae* fell into disuse and the dye disappeared from the markets of the world until the 17th and 18th centuries when it again took on the aspects of an industry, and the "Weed" became an article of international trade.

b) *Blue and Red Dyes.* About 1300, a Florentine merchant named Federigo (19), while in the Levant, noted that urine imparted a very fine color to some plants. On returning home, he experimented with successful results and founded the lucrative dye industry which established his family name, the Orcellarii, Ruccellarii or Rucellae, and gave to his native city a monoply that existed

until the discovery of the Cape Verde Islands. This, or possibly the Spanish term for the plant, "Orcigilia", is thought to be the origin of the botanical name Roccellaceae. Though the early source of supply was the Levant and the Mediterranean countries through Florence, discoveries of new lands revealed the abundance of this lichen on rocks along warm sea coasts, and the trading centers became successively Montpellier and Holland. The Canaries, as well as the Cape Verde Islands, Cape of Good Hope, Angola, East Africa, Mozambique, Madagascar, Zanzibar, Ceylon, the East Indies and Australia; then in the New World, Valparaiso and Lima as well as the West Coast of North America, became the successive sources of the "weed". Importers have always been averse to disclosing the origin of their best supplies, but *R. tinctoria* of the Cape and South America was larger ("6–8 inches long, and as thick as goosequills") and so preferred by the trade (203). In 1750 the Cape Verde and Canary Islands exported 100 tons annually to England. In 1818 this cost from £40 to £200 a ton, depending on the quality (19), but by 1886 *R. tinctoria* gathered in Ceylon off palm stems had fallen to £50 a ton (143). The last figures available list the importation of tanning and dyestuffs into England for 1935 (88) as Annatto, 837,919 pounds; Brazilwood, 854,581 pounds; Cudbear (including orchil) Lichen dyestuffs, 411,265 pounds.

The chemical nature of *Roccella* dye was not understood in the early days of the industry and this was further complicated by trade secrets and tradition. In the old English method, the lichen was cut small or reduced to a powder by passing it through a sieve, and placed in iron drums provided with stirrers. It was then moistened slightly with stale urine, the mixture being stirred once a day with additions of soda for 5–6 days at a temperature of 35° to 45° C. Fermentation proceeded and was checked frequently until the coloring matter, a dove gray, ceased to increase. The product, Orchil Paste, was then placed in wooden casks and covered with a sufficient quantity of lime water or gypsum solution until needed by the dyer. To make Orchil liquor, the lichen was treated with water and urine and permitted to ferment as for Orchil Paste after which the fibrous matter was removed and the liquor collected and stored. Sal ammoniac, sal gem and saltpetre were sometimes used in the process (108).

Dillenius in 1741 said of its color "that it was reckoned more beautiful when first dyed, than the Tyrian Blue", while Bancroft (19) describes the infusion of Orchil as of a red crimson inclining to violet.

Modern methods were based on a more accurate knowledge of the chemistry of the lichen dye. According to Hill, the lichen is sprayed with ammonia in the air until the mass turns color, when the blue orchil liquor is extracted with water; if heated until the ammonia is driven off, red orchil results; afterwards the plants are dried and ground to a fine powder.

The French (19) employed a crustaceous species commonly called "perelle" to obtain a purple-blue dye. M. Cocq, in the 81st volume of the Annales de Chimie, describes its preparation as observed at Clermont, France. The lichen is macerated in wooden troughs, six feet long, three feet wide and two feet deep, fitted with tight covers. Two hundred pounds of perelle and two hundred and forty pounds of urine are mixed in this trough and stirred for three hours for two successive days and nights. The cover is removed only for stirring in order to retain as much as possible the volatile alkali (ammonia) of human urine. On the third day, ten pounds of sifted and slaked lime are added and well mixed together with a quarter-pound of arsenic and an equal weight of alum. The mass is then stirred repeatedly several times, once every quarter-hour; later, every half-hour until fermentation is established to prevent the formation of a crust on the surface. In forty-eight hours, fermentation is renewed by adding two pounds of sifted lime and stirring continually, once every hour until the fifth day. On the eighth day, it is stirred every six hours, extending the process a fortnight or three weeks. The coloring matter is kept moist in closed casks until used. It is said to improve the first year, suffers little change during the second year, and begins to deteriorate in quality on the third year of storage.

Dr. Bancroft (19) recommended the use of ammonia over urine and pronounced the addition of arsenic and alum as useless and dangerous while suggesting that hogsheads would facilitate agitation without the need of removing the cover of the container.

c) *Brown and Yellow Dyes.* Employment of brown and yellow dyes is an old custom in the northern countries of Europe. Fries remarked on the use of the class, Lichenes, in the Arts "that almost

all that is known has been owing to the Northern—the Anglo-Saxon, Scandinavian and German Nations whom necessity constrained to value and improve all of Nature's gifts". In certain districts of Scotland as late as 1855 (115), almost every farm and cotterhouse had its tank or barrel of "graith" or putrid urine (the form of ammoniacal liquid employed) and its "lit-pig" wherein the mistress of the household macerated some familiar "crottle" (Scotch vernacular for lichens in general) to prepare dyes for their homespuns. The usual practice was to boil the lichen and woolen cloth together in water or the urine-treated lichen and cloth until the desired color was obtained. This took several hours or less on the addition of acetic acid, producing fast dyes without the benefit of a mordant or fixing agent. The dye substance had no deleterious effect on the wool. The color would be intensified by adding salt or saltpetre. This method was used not only in Scotland but also in Iceland, for those homespuns best known to the trade as "Harris Tweed" (78). Horwood (94) states that in the Shetlands the lichens are harvested in May or June or after rain in the autumn or winter, using a metal scraper for obtaining the rock species. These are washed, dried in the sun and sometimes powdered. To this powder is added quicklime and water, including ten pounds of lichen to a half pound of sal ammoniac and then permitting the mass to ferment in a covered vessel for a few days. These lichens were sometimes prepared for the London market and shipped in casks as "cudbear". The term is derived from a corrupt pronunciation of the name of Dr. Cuthbert Gordon, a chemist of Glasgow, who obtained a patent for his process in preparing the dye from *Ochrolechia tartarea* on a large scale. It is said that one person could collect 20–30 pounds daily, any one locality being visited every five years (19). The lichens were washed and dried, reducing their weight by half. The peasants of Westmoreland and Cumberland gathered this species for dyes at the rate of one pence per pound, while manufacturers of woolens and silks paid ten shillings a hundredweight for it with a profit to the middleman of eight pence. For storage purposes the lichen was mixed with aqua ammonia from human urine or pounded with stale chamberley, salt or kelp. The coarse paste was then rolled into small balls or cakes with lime or burnt shells. These were wrapped in dock leaves and hung up to dry in peat smoke, which accounts for the odor peculiar to "Harris Tweed". In this fashion,

it would keep for a year or more and when needed it was redissolved in warm water.

The color of Cudbear and Orchil is so similar as to be commercially indistinguishable. They dye best in a neutral bath producing a bluish-red or dull magenta shade but were frequently applied with sulfuric acid in conjunction with other vegetable dyes and coal tar dyes, especially magenta (140). Addition of indigo and the dye of lungwort would give a permanent black dye; while *Roccella tinctoria* was used as the first dye for blue British broadcloth, having a purple tint against light. A variety of colors and shades could be obtained by the use of different species or varying the treatment with oil of vitriol, logwood or chemicals. Thus acids produced yellows, alkalies produced blues, lead acetate gave a crimson precipitate, calcium chloride a red precipitate, stannous chloride a red then yellow, while alum was more generally used by the country folk for reds. The color of cudbear was said to possess great beauty and lustre at first, but quickly faded and should never be employed unless for the purpose of giving body and lustre to blue dyes as indigo ("bottoming") or as a ground for madder reds (115). In deep shades, the color has an intensity and body which cannot be equalled by coal-tar substances, and though they are not fast to light or milling and scouring, they do resist soaping, becoming bluer (108). Silks, and occasionally linens, had the dye applied in a soap solution with or without acetic acid, and though still in use this method has been superseded in a large measure by synthetic dyes. Lichen dyes have not been applied to cotton cloth.

Cudbear and Orchil have both been used in Holland for the manufacture of litmus, known to the French as "tournesol". The dye is first prepared, after which gypsum or powdered chalk is added and the mixture cast into small, purplish-blue cubes once sold as "lacunus". This, when dissolved in water and soaked up in unsized paper, was retailed as litmus paper. The early product was rather unstable and tended to become colorless. This was thought to be due to micro-organisms, so that alcohol or chloroform was often added when the litmus was kept in liquid form. Tincture of Cudbear is still used in the drug trade, though since the Dutch source of supply is no longer available, it has been necessary for the U. S. Pharmacopoeia to substitute a coal-tar derivative, amaranth (187).

d) *Chemical Properties of Dye Lichens.* Dyeing properties of lichens are due to the presence of lichen acids, some of which afford the chromogens from which the coloring matter is derived. Keegan reports its development as an excretion in the outermost part of the lichen thallus and the upper side of the apothecia, or in general, those parts of the plant best exposed to the air at all times of the year and at all latitudes. This is of interest, since tradition would have the best colors produced from late fall harvests. The lichen acid occurs as an ester and a result of the symbiotic condition of these plants, the fungus component being the sole seat of the product, though Keegan says it cannot develop the acid by itself. He found that when the quantity of proteins decreases in the lichen the quantity of acid increases. As the alga borrows proteins from the fungus, a powerful process of oxidation is inevitable in the fungus. The alga would use the nitrogenous group of the protein molecule, the aromatic groups not needed would be left behind in the fungus. According to Keegan, then, the acids originate by a mechanism of deassimilation (oxidation) provoked by a penury of nitrogen in the vicinity of the algal cells; it would appear that formation of these acids is not as simple or direct as that of tannins or other chromogens of higher plants. The blue-purple litmus would be due to the addition of an inert nitrogen atom to the molecule which serves to check the otherwise natural tendency of orcinol on higher oxidation to assume a typical red or brown shade (106). In the Roccellaceae there are two different coloring substances, erythrin and lecanoric acid. When treated with ammonia, the acids are apparently split to orcin and carbonic acid, the orcin under the influence of oxygen, yielding orcein which is the coloring principle of orchil.

Cosmetics and Perfumes.

a) *History.* Since the 16th century, members of the families Cladoniaceae, Stictaceae, Parmeliaceae and Usneaceae have been used as raw materials in the perfume and cosmetic industries. At first this consisted of drying and grinding the plants to a powder and combining them crudely with other substances, but as the manufacturers became more expert in their trade, these materials were skillfully combined into toilet powders and scented sachets of high value. Amoreux (2) records the use of *Evernia prunastri,*

though *Evernia furfuracea* and *Lobaria pulmonaria* possess similar aromatic substances and were also used. The lichens sought for these purposes were known under a variety of names, as "Lichen quercinus viridis", "Muscus arboreus, acaciae, and odorante", "Eichenmoos" and most commonly as "Mousse de Chêne" or Oak-moss and Scented-moss (77). *Ramalina calicaris* was used in place of starch to whiten hair in the dye of wigs and perukes. Cyprus Powder, a combination of *E. prunastri, Anaptychia ciliaris* and *Usnea* species, scented with ambergris and musk, oil of roses, jasmine, or orange blossoms, was celebrated in the 17th Century as a toilet powder that would whiten, scent and cleanse the hair (198). After a somewhat lengthy eclipse, these plants reappeared as raw stuffs for perfumery, owing to the creation of scents with a deep tone and to the demands for the very stable perfumes of modern extraction for which purpose they are almost universally used to this day.

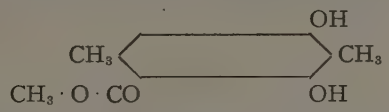
The principal species used today in perfumes and cosmetics include *Evernia prunastri, E. furfuracea, E. mesomorpha, Ramalina fraxinea, R. farinacea, R. pollinaria* and others of the Ramalinae, though when this group is included in the mass it serves to depreciate the value of the former. *Lobaria pulmonaria* (Mousse de la base du Chêne) is used to some extent, though it is considered a more costly substance, perhaps due to the fact that in Europe it is confined to subalpine woods and is, therefore, scarcer (159). The true Oak-moss (*E. prunastri*) of Europe is collected in shaded, damp habitats occurring in all parts of France, especially in the central mountain ranges, in the Alps and in the neighborhood of Paris, the most valued coming from the Forest of Fontainebleu; also from the forests of Czecho-Slovakia, of Herzegovina and the Piedmont of Italy (93). Not only the source but the substratum is given a great deal of attention by the perfumer who differentiates between those plants that grow on oak (greenish) and those found on conifers (greyish); in the latter case rightly so, since resins may be included with the lichen, rendering it less desirable for the trade. In all instances the crop is gathered by peasants or by shepherds, as in Jugoslavia, and pressed into large bales for export. The American supply is derived from these sources, importations amounting to a few tons yearly at a cost of from five to seven and one-half cents a pound delivered in New York City. Since the

present war has cut off the supply, a few companies, formerly established in France and Holland, have been interested in developing the American market, but the lack of apt collectors willing to work in competition with Europe's cheap labor or even at a somewhat higher rate per pound renders the commercial possibilities somewhat doubtful. Experiments including a number of American species have been carried out with little success except in the case of those traditionally used in the Old World, and of these there are sufficient quantities available in the northern part of the United States and Canada and at the lower altitudes on the higher hills (2000 feet elevation).

b) Chemical Properties of Essential Oil of Lichens. Use of dried, pulverized Oak-moss in the perfume industry is restricted, the principal sale being of extracts, essences and "resinoids". Gildermeister and Hoffmann state that the method involves exhausting the lichen by means of a volatile substance and treating with acetone, which removes the resins, waxes and chlorophyl. The extraction by alcohol gives an "extract of Oak-moss" which may be used in this form or may be concentrated in order to obtain a semi-fluid substance. Research on the part of French and German chemists during the last thirty years has revealed much of the chemical nature of the extracts, gums and mucilages produced by these lichens. Gattefossé (75) made a study of the essential oils and alcoholic extracts of all those lichens which were utilized as Oak-moss, and by extraction and distillation obtained data that caused him to conclude that oil of Oak-moss was almost exclusively a compound of phenol called lichenol, considered an isomeric compound of carvacrol. These results were verified by St. Pfau who further expressed the opinion that sparrassol, a metabolic product of the fungus *Sparassis ramosa,* is identical with methyl everninate resulting from the alcoholysis of everninic acid, and is present in proportions of about 2.8% with a characteristic anise seed odor.

Walbaum and Rosenthal questioned the findings of Gattefossé; so they distilled by steam the oil of Oak-moss from *Evernia prunastri.* This, at ordinary temperature, formed an oily crystalline mass of a dark color with a very powerful and agreeable odor. Upon further analysis, it was found that Gattefossé's discovery was founded upon an error, and that not lichenol ($C_{10}H_{14}O$) but orcinol monomethylether is the principal constituent of Oak-moss. This

phenol, though not the main odoriferous part of Oak-moss oil, has a pleasant, creosol-like smell, and an ester, β-orcinol methyl carbox-



ylate ($C_{10}H_{12}O_4$), which does not enter into the odor of the lichen oil. In the resinous precipitate, Walbaum and Rosenthal found ethyl everninate generated only during extraction through esterification of the everninic acid ($C_{17}H_{16}O_7$) which they stated occurred in the free state in the lichen, and that during boiling with baryta water it split into orcinol and everninic acid with liberation of carbon dioxide. This acid is closely related to orcinol monomethylether and would be converted into it by the liberation of carbon dioxide. For these reasons Walbaum and Rosenthal felt that the genesis of the principal constituent of the odoriferous substances of Oak-moss had a close connection with the origin of evernic and everninic acids. Recently, Stoll and Schener found in the volatile fraction some compounds which may also have a function in producing this odor, mainly thujone, naphthalene, borneol, camphor, civeole, citronellol, guaniol, vanillin, methylnonylketone and stearic aldehyde.

The multiplicity of types of essences and extracts is due in part to the diversity of substrata on which these lichens grow as well as to the varying mixtures of species offered to the manufacturer in the lot, and the mode of extraction. This is indicated by Hesse (85) who had extracted atranorine and everninic acid from a sample of *Evernia prunastri* on oak but not from samples collected on beech or birch, while a sample from a lime-tree yielded some usnic acid. The whole problem is further complicated by the fact that most constituents of Oak-moss react upon the solvent. Treatment of lichen extracts with alcohol is seldom employed for preparation of essences, since it alters the evernic acid. Thus the lichenol obtained by Gattefossé using this method was everninate of ethyl. Synthesis of everninic acid, divarine and others has been performed in the laboratory but apparently has not been applied on a commercial scale.

Horel states that in the trade, the oil is extracted by means of low boiling solvents, after which it is purified and decolorized,

the process yielding 0.2–0.3 kilogram of the raw extract or 20–30 grams of the pure essential oil from different technique of extraction in which 100 grams of the dried lichen yielded 8.5 grams of crude everninic acid.

c) Uses of Essential Oils. The essential oil of Oak-moss or "concrete" is used in soap making in its natural condition, as an impalpable powder or in the form of resinarome. The powder form permits production of soap-balls agreeably scented and at a reasonable price, but unless the manufacturer obtains a perfectly impalpable powder, the soap-balls give the impression of being made from sand. In order to maintain the quality of his product, the soap maker must establish connections with a reliable purveyor. To be sufficiently scented, a soap-ball must have 1 or 1½% by weight of powder to soap. When used for this purpose, Oak-moss improves, strengthens and cheapens lavender-scented products. It is essential in the finer grades of cosmetics in combination with jasmine, tuberose and orange blossom scent. Parry suggests the use of *Cladonia rangiferina* and *Cladonia sylvatica* for purposes of retaining odor, since they are whitish, easily dried and abundant in open healthy places. Some, as *Sticta fuliginosa* and *Sticta sylvatica,* have objectionable odors that are easily recognized by their fishy or methylamine nature. Mention has already been made of the many uses of Iceland Moss in foods and medicines. In the cosmetic field, it serves as a source of glycerol in the soap industry and in the manufacture of cold creams, though it is odorless (166).

Lichens are especially adapted for perfumery, since to the parfumeur the peculiar reciprocity of the components forming the lichen unit and known to the unromantic biologist as "symbiosis" is an example of harmonious action. Therefore, the extract of Oak-moss or Scented-moss "agrees" and "harmonizes" in the happiest manner with a large number of other essences. Its fragrance has been likened to musk-lavender and as such it may be used as a fixative (of the poppy type) blending well with bergamot, citron, acetate of lynalyl and linalol, thus supplying freshness; with neroli, jasmin, rose and cassia, it improves the flavor of these flowers; it gives flexibility to taragon, coriander, portugal, ylang-ylang and vanillin; contributes stability and depth to patchouli, vetyver, coumarin and musk, and elevation to alpha ionene.

It also blends well with synthetic oils, as amyl and isobutyl salicylate and aceto-phenone (141, 169). It is indispensable as the basis of numerous perfumes, such as Chypre, Fern, Heath, and many bouquets called "Fancy", as well as for the Oriental perfumes.

Miscellanea

Gums. The dyeing and paper industries have need for quantities of sizing with which to dress and stiffen silks, print and stain calico and size paper. During the Napoleonic Wars, because of the French monopoly of Senegal Gum, the celebrated English inventor, Lord Dundonald, attempted to introduce lichen mucilage in place of the French product, but there is no evidence that he succeeded in interesting the English market. At Lyons the French appear to have successfully used lichen mucilage as a substitute for gum arabic in the fabrication of dyed materials (82). The problem has been opened more recently by Minford (146) who reports that Iceland Moss and some other lichens may be prepared as light-colored, transparent and high-grade gelatin, isinglass and similar gelatinous products corresponding to those obtained from vegetable products for this purpose.

Injury by Lichens. Lichen injury to artificial structures has been already discussed in relation to damage of stained glass windows of churches (144). Cengia-Sambo (26) reports an interesting incident of stains and incrustations on marble, alabaster and Florentine mosaics resulting from the activity of lichen growths favored by humidity.

Orchardists and silviculturists have long been interested in the probable relationship of lichens to trees. Many sprays, including Bordeaux Mixture, caustic soda and light-boiling tar oils (65), have been recommended for the removal of these "unsightly if not injurious plants" on the grounds that they could hardly be considered as timber preserving plants. Indirectly they may cause an economic loss by serving to shelter the many injurious insects that seek cover and lay eggs. Kaufert notes that the bark of *Populus tremuloides* remains permanently smooth through the presence of a persistent periderm. If injured by fungi, lichens or mechanical injury, the bark may be stimulated to develop rough fissures, since these injuries appear to be associated with rough bark on some aspen stands. In studying the influence of *Usnea*

sp. upon trees in South Africa, Phillips concluded that in this case the lichen is definitely detrimental in that its fungal component is parasitic upon tissues external or internal to the cork cambium. Vigorous crowns as well as defective ones may be infected. Since the lichen cannot develop luxuriantly under the conditions obtaining in undisturbed high forests, he recommended that the forest canopy be preserved as a means of inhibiting the rampant growth of this lichen. Wellborn suggested that some leaf spots of the coffee plant may be caused by a lichen. Howbeit, the whole problem of whether lichens injure the trees on which they are fastened cannot be solved, as Fries once remarked, "by mere denial".

APPENDIX. LICHENS EMPLOYED IN DYEING AND MINOR USES[11]

SCIENTIFIC AND COMMON NAMES	REGIONS* WHERE FOUND OR GENERALLY USED	COLORS OBTAINED	USES
Alectoria jubata (L.) Ach. Horsehair lichen	England	pale green, brown-red	woolens (135)
Bacidia muscorum Mudd	Europe	red	woolens (114)
Borrera ashneyi (?)	Chutcheleera, India	flesh-color	woolens (135)
Caloplaca murorum (Hoffm.) Th. Fr.	Sweden	yellow	woolens (90, 114)
Candelaria Mass.	Sweden	yellow	candles (198)
Candelariella vitellina (Ehrh.) Müll. Arg.	Sweden	yellow	woolens (114)
Cetraria aculeata (Schreb.) E. Fr.	Canary Is., Scotland	red-brown	woolens (135)
C. fahlunensis (L.) Schaer. Swedish shield lichen†	Europe	red-brown	woolens (114)
C. glauca (L.) Ach. Pale shield lichen†	Europe	chamois	woolens (90)
C. islandica (L.) Ach. Iceland moss	Iceland	brown (1), yellow (2), red-brown	woolens (135) leather (7)
C. juniperina (L.) Ach. En-mossa, cedar lichen†	Scandinavia	yellow	woolens (135)

* Region given does not represent full range of any one species, most of these are cosmopolitan.

† Common names from Nearing.

[11] Synonymy brought to date where possible according to Zahlbruckner (232) and Fink (63).

Scientific and Common Names	Regions* Where Found or Generally Used	Colors Obtained	Uses
C. nivalis (L.) Ach. Snow lichen†	Europe	violet	woolens (114)
C. pinastri (Scop.) S. Gray Pine lichen†	Europe	green	woolens (90)
Cladonia coccifera (L.) Willd. British Soldiers	Europe	red-purple	woolens (114)
C. fimbriata (L.) Willd. Trumpet lichen†	Europe	red-purple	woolens (114)
C. gracilis (L.) Willd. Spoon lichen†	Europe	ash-green	woolens (114)
C. rangiferina (L.) Web. Reindeer moss	Europe	iron-red	woolens (114)
C. pyxidata (L.) Hoffm. Goblet lichen†	Europe	ash-green	woolens (114)
Dermatocarpon miniatum (L.) Mann	Europe	ash-green	woolens (114)
Evernia furfuracea (L.) Mann Sprout lichen†	Europe	red-brown	woolens (114)
E. prunastri (L.) Ach. Oak moss	Europe	violet	woolens (114)
E. vulpina (L.) Ach.	Scandinavia	yellow	woolens (198)
Gyrophora cylindrica (L.) Ach. Rock tripe	Iceland	green-brown	woolens (135)
G. deusta (L.) Ach. Rock tripe	Sweden	violet	paint ("Tousch") (119) woolens (114)
G. vellea (L.) Ach. Rock tripe	Sweden	violet	woolens (114)
Haematomma ventosum (L.) Mass. Black Lecanora, Bloody spotted Lecanora	Scotland	red-brown	woolens (135)
Lecanora calcarea (L.) Nyl.	Sweden	red-brown	woolens (2)
L. parella Mass. Light crottle, Crabseye lichen	Gt. Britain France	violet	woolens; Orseille d'Auvergne (135)
Lepraria chlorina (DC.) Ach. Brimstone colored Lepraria	Scandinavia	brown	woolens (135)
L. iolithus (L.) Ach. Viol-massa (Swedish)	Scandinavia	brown	woolens (135)
Lobaria scrobiculata (Scop.) DC.	Scotland England	brown	woolens (135)

* Region given does not represent full range of any one species, most of these are cosmopolitan.

† Common names from Nearing.

Scientific and Common Names	Regions* Where Found or Generally Used	Colors Obtained	Uses
Aik-raw, Oak rag, Warty leather lichen†			
L. pulmonaria (L.) Hoffm. Oaklung, lungwort, Aikraw, Hazelraw, Hazelcrottle, Rage, Stane Raws	Scandinavia Gt. Britain	orange, brown	wool; (+indigo = lasting black) (135)
Mycoblastus sanguinarius (L.) Norm. Red fruited lecidea	Scotland	red-purple	woolens (135)
Nephroma parile Ach. Chocolate colored Nephroma, Powdery Swiss lichen†	Scotland	blue	woolens (135)
Ochrolechia tartarea (L.) Mass. Crotal, Crottle, Cockur, Corcir, Korkir	Scotland and adjacent islands Sweden, France	purple-crimson, blue	Cudbear (19), tincture of cudbear (187), (+logwood = red-purple) litmus
Parmelia acetabulum Duby	North Ireland	brown, orange	wool, homespuns, Harris tweed (135)
P. caperata (Hoffm.) Ach. Stone crottle, Arcel, Wrinkled shield lichen†	Isle of Man	brown-orange, lemon, yellow	woolens (135)
P. centrifuga (L.) Ach. Ring lichen†	Gt. Britain	red-brown	woolens (90)
P. conspersa (Ehrh.) Ach. Sprinkled parmelia, Boulder lichen†	England	red-brown	woolens (135)
P. Kamtschadalis (?)	India	pale rose	to print and perfume calico cloth (143)
P. olivacea (L.) Ach. Bronze shield lichen†	Gt. Britain	brown	woolens (143)
P. omphalodes (L.) Ach. Smoky shield lichen,† Black crottle, Corks, Cockur, Crostal	Scandinavia Scotland Iceland	purple, crimson	woolens (135)
P. physodes (L.) Ach. Dark crottle, Puffed shield lichen†	Scotland Scandinavia	brown	woolens (19)
P. saxatilis (L.) Ach. Stane raw, Scrottye, Stenlaf (Swedish)	Scandinavia Gt. Britain	dirty orange, yellow, red-brown	woolens (19) wool (176)

* Region given does not represent full range of any one species, most of these are cosmopolitan.

† Common names from Nearing.

Scientific and Common Names	Regions* Where Found or Generally Used	Colors Obtained	Uses
P. stygia (L.) Ach. Midnight lichen†	Gt. Britain	brown	woolens (143)
Peltigera canina (L.) Willd. Dog lichen†	Europe	iron-red	woolens (114)
Pertusaria pseudocorallina (Sw.) Arn. Westring's Isidium	Norway Sweden	red-purple	woolens (135)
P. corallina (L.) Arn. White crottle	Scotland	red-purple	woolens (135)
Physcia pulverulenta (Schreb.) Nyl. Mealy Blister lichen†	Europe	yellow	woolens (143)
Ramalina calicaris (L.) Röhling Common Twig lichen†	Europe	yellow-red	woolens (114)
R. cuspidata (Ach.) Nyl.	Europe	light brown	woolens (176)
R. farinacea (L.) Ach. Mealy Ramalina	England	light brown	woolens (135)
R. fraxinea (L.) Ach. Ash Twig lichen†	England	gray-white	woolens (114)
R. scopulorum Ach. Ivory-like ramalina	Scotland	red-brown	woolens (135)
Rhizocarpon geographicum f. *atrovirens* (L.) Mass. Map lichen	Scandinavia	brown	woolens (135)
Roccella fuciformis (L.) Lam. and DC. "Lima" weed, "Angola" weed Orcella, Orcigilia; Orchil	France England	purple-crimson, red-yellow	Orchil, litmus; wool, silks, feathers, carpet yarns; and staining wood and marble (49, 91)
R. Montagnei Bél. Orcella weed	Germany, Italy	(+ other dyes = brown, maroons, claret)	white wine; and with indigo (140, 108)
R. phycopsis Ach. Archil	Burma	blue	for British broadcloth; tincture of alcohol for thermometers (143)
R. tinctoria Lam. and DC. Orseille (Valparaiso Weed)	South France	purple-crimson	"bluing" agent

* Region given does not represent full range of any one species, most of these are cosmopolitan.

† Common names from Nearing.

Scientific and Common Names	Regions* Where Found or Generally Used	Colors Obtained	Uses
Solorina crocea (L.) Ach. Saffron-yellow Solorina	Scotland	yellow	woolens (135)
Stereocaulon paschale (L.) Hoffm. Eastern lichen†	Europe	ash-green	woolens (114)
Sticta aurata Ach. Rose & gold lichen†, Lungwort Hazelraw, Hazel crottle	Gt. Britain Scandinavia	saffron, brown	woolens (135)
S. crocata (L.) Ach. Rags, Oakrag, Gold Edge licken†	Scandinavia Gt. Britain	gamboge, brown	woolens (135)
Teloschistes parietinus (L.) Norm. Wäg-laf (Swedish)	England Sweden	yellow	woolens (135) Easter eggs (135)
T. flavicans (Swartz) Norm. Yellow Borrera	Germany	gamboge, yellow	woolens (135)
Umbilicaria pustulata (L.) Hoffm. Blistered umbilicaria	Norway Germany	red, purple, brown	woolens (119) black paint (43)
Urceolaria calcarea Sommerf. Corkir, Limestone Urceolaria	Gt. Britain Western Islands	red-crimson	woolens (135) cudbear (49)
U. cinerea Sommerf. Greyish Urceolaria	England	red-crimson	woolens (135)
U. scruposa (Schreb.) Ach. Rock Urceolaria	England	red-brown	woolens (135, 143)
Usnea barbata (L.) Wigg. Bearded Usnea, Old Man's Beard†	S. America Pennsylvania, U.S.	orange-red	woolens (19)
U. florida (L.) Web. Flowering Usnea	Europe	green-yellow, red-brown	woolens (135)
Usnea plicata (L.) Wigg. Plaited Usnea	Europe	green & yellow	woolens (114)
Usnea sulphurea Th. Fr.	Falkland Is.	brown	woolens (3)
Variolaria orcina Ach.	France	violet	woolens, orchil (140)
Xanthoria candelaria (Ach.) Arn. Ljas-mässa (Swedish) (= *Teloschistes candelarius*. (L.) Fink)	Sweden	yellow	woolens (143)

* Region given does not represent full range of any one species, most of these are cosmopolitan.

† Common names from Nearing.

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Proposed Future Contents of
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Articles received and awaiting publication

Root-rots of Some Non-cereal Crops	G. H. BERKELEY *Dominion Laboratory of Plant Pathology*
The Classification of Inflorescences	H. W. RICKETT *New York Botanical Garden*
The Inferior Ovary	GERTRUDE E. DOUGLAS *New York State College for Teachers*
Control of Noxious Plants	H. K. WILSON *University of Minnesota*
Classification of the Green Algae	F. E. FRITSCH *University of London*
Recent Studies on the Inheritance of Size and Shape in Plants	H. H. SMITH *Bureau of Plant Industry*

Articles arranged for most recently

Endomitosis	A. LORZ *Seton Hall College*
The Male Gametophyte of Angiosperms	A. GERSHOY *University of Vermont*
Techniques for Aseptic Growth of Plants	L. C. KNORR *Cornell University*

Articles in course of preparation

The Cytology of Fertilization in Angiosperms	L. E. ANDERSON *Duke University*
Development of the Madro-Tertiary Flora	D. I. AXELROD *University of California*
Relation of Wood Anatomy to Taxonomy	I. W. BAILEY *Harvard University*
Anthocyanin Pigments	F. BLANK *Switzerland*
The Genetics of Pollen Tube Growth	J. T. BUCHHOLZ *University of Illinois*
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